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A New Genus for South American Snakes Related to *Rhadinaea obtusa* Cope (Colubridae) and Resurrection of *Taeniophallus* Cope for the "*Rhadinaea*" *brevirostris* Group

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ABSTRACT

Psomophis, new genus, is erected to accommodate three species of South American colubrid snakes: *Rhadinaea obtusa* Cope, 1863 (type species), *Enicognathus joberti* Sauvage, 1884, and *Liophis genimaculata* Boettger, 1885. The last species is here resurrected from the synonymy of *joberti*. These snakes differ from all other South American colubrid genera in the combined characters of small size, high number of ventral scales, midbody scale rows 17 or 19 with lateral reduction posteriorly, distinctively shaped premaxillary bone, and peculiar hemipenis.

The hemipenis is deeply bilobed, lacking apical discs, with the lobes individually capitate (bicapitate) and pseudocalyculate (becoming acalyculate upon eversion); the lobes bear large spinulate papillae (soft spines) on the sulcate sides but are nude on the asulcate sides; the organ is spinose proximal to the lobes; the sulcus spermaticus is deeply forked and centrolineal. *Psomophis* probably is allied with a large group of South American "xenodontine" colubrids, but relationships among most genera within that assemblage are presently unclear.

The species of *Psomophis* are most likely to be confused with species of the "*Rhadinaea*" *brevirostris* group (sensu Myers). Possible relationships of the *brevirostris* group to the "*Liophis*" or "*Rhadinaea*" *undulata* group (i.e., *Echinanthera* Cope, sensu stricto) remain to be investigated, inasmuch as a recent claim of hemipenial synapomorphy cannot be corroborated. Rediscovery of *Lygophis nicagus*—nominal type species of the unused name *Taeniophallus* Cope—allows, for present purposes, convenient resurrection of *Taeniophallus* for the *brevirostris* group. The new genus *Psomophis* differs in fundamental hemipenial and other characters from *Echinanthera* and *Taeniophallus*.

Reasons are footnoted for a few incidental taxonomic conclusions on Neotropical xenodontines, including (1) suggested removal of *Pliocercus* (coral snake mimics) from the synonymy of *Urotheca*, an apparently monophyletic sister group, and (2) removal of the genera *Saphenophis* and *Tropidodryas* from the tribe Pseudoboini, which is returned to Bailey's 1967 concept.

INTRODUCTION

The Neotropical snake genera *Rhadinaea* and *Liophis* historically have accommodated many species of relatively generalized terrestrial colubrids. They are among the largest genera of Neotropical colubrids, each with more than 30 recognized species according to recent revisions (Myers, 1974; Dixon, 1980). Myers (1969, 1973) had provisionally transferred several species previously assigned to these and other genera to *Lygophis* (= *Liophis* sensu Dixon) before erecting the genus *Saphenophis* to hold them. Myers (1974: 22) similarly excluded several other enigmatic species from *Rhadinaea* by transferring them temporarily to *Liophis*, which was taxonomically confused anyway:

> Certain species that have been referred to *Rhadinaea* by other authors actually are not assignable to any genus as presently defined. Three of these species—*genimaculata* Boettger (=*joberti* Sauvage), *obtusa* Cope, and *steinbachi* Boulenger—are under investigation and can conveniently (but improperly) be included in the genus *Liophis*, where they also have been placed by various authors. Also in this category is "*Liophis*" *undulatus* and its several relatives, which comprise an undescribed genus according to Joseph R. Bailey (personal commun.), who has data on the group.

Dixon (1980) necessarily referred the above species to incertae sedis during his process of redefining *Liophis*. Since then, Di-Bernardo (1992) has properly resurrected *Echinanthera* Cope for the *undulatus* group (but see below), and Myers and McDowell (in manuscript) have clarified the relationships of "*Rhadinaea*" *steinbachi*.

Since 1974, it has seemed evident that the remaining epithets mentioned above—*genimaculata*, *joberti*, and *obtusa*—belong to spe-

cies in a small monophyletic group in need of a new generic name. There was uncertainty, however, over the interpretation of particular hemipenial features based solely on dissection of retracted organs. But an everted hemipenis is finally available and a generic name and synopsis of the species are presented herewith.

Some of the nomenclatural changes referred to above require us to be explicit about usage of generic names. We use *Liophis* in the sense of Dixon (1980) and Myers (1986), as the plesiomorphic member of the tribe Xenodontini. Unless qualified by "s.l." (sensu lato), we currently use the name *Rhadinaea* in a revised sense to refer to all species of *Rhadinaea* sensu Myers (1974) *except* for the eight Central and South American species of Myers' *lateristriga* group[3] and the six South American species of his *brevirostris* group.

There is potential confusion between species of the new genus and members of the "*Rhadinaea*" *brevirostris* group, which was placed in *Echinanthera* by Di-Bernardo (1992). Although we have been aware for some time that *Echinanthera* is an available name for the "*Liophis*" *undulatus* group—which therefore is not a "new" genus[4] as thought by Bailey (vide supra)—we disagree with Di-Bernardo's stated reasons for including the "*Rhadinaea*" *brevirostris* group within a resurrected *Echinanthera* (see below, Remarks under *Taeniophallus*). Therefore, we shall use the name *Echinanthera* in its strict sense, that is, for the nominal species that seem closely related to the generic type (*Aporophis cyanopleurus* Cope), including *E. amoena*, *E. cyanopleura*, *E. melanostigma*, and *E. undulata*.

Nonetheless, the *brevirostris* group should not be maintained in *Rhadinaea*. Myers (1974: 232, 236) stated that,

> the taxonomic position of the *brevirostris* group should be re-evaluated as data become available on the systematics of other groups of South American colubrids . . . The possibility should also be kept in mind that the *brevirostris* group might have been independently evolved from alsophiine ancestry—although reasonably conclusive evidence should be presented by anyone wishing to remove that group from *Rhadinaea*.

Support for removal of the *brevirostris* group from *Rhadinaea* subsequently was provided by Cadle (1984a, 1984b), whose immunological studies of serum albumins demonstrated that the large assemblage commonly referred to as xenodontines consists principally of two large Neotropical clades, one primarily Central American, the other South American. Moreover, those data suggested substantial evolutionary and temporal divergence between members of the two clades (Cadle, 1984c, 1985). With respect to *Rhadinaea*, the immunological data demonstrated a clear association of most species with the

[3] The *Rhadinaea lateristriga* group = *Urotheca* sensu stricto, an assemblage of curiously patterned xenodontines that share hemipenial and caudal resemblances (now perceived as synapomorphies) with vividly ringed coral snake mimics of the genus *Pliocercus* (Myers, 1974: 230, 233; Savage and Crother, 1989). Although Savage and Crother (op. cit.) properly addressed one of the problems of paraphyly in Myers' revision of *Rhadinaea*, we disagree with their submerging of *Pliocercus* in the synonymy of *Urotheca*.

Present evidence suggests that *Pliocercus* and *Urotheca* s.s. are monophyletic sister groups—each of which is characterized by synapomorphies of color pattern, including *Micrurus*-like rings in the former and a longitudinal white line(s) in the latter. Absence of the last character in a few nearly unicolor species was attributed to secondary loss by Myers (1974: 231), who based his conclusion on the seemingly vestigial remnant of a pale line on the neck of *dumerilii* and on the evidently atavistic occurrence of a pale line in some specimens of *fulviceps*. Thus, there is no indication that *Urotheca* s.s. is paraphyletic with respect to *Pliocercus*. Inasmuch as the evolutionary history of *Pliocercus* is linked via mimicry complexes with venomous coral snakes (Greene and McDiarmid, 1981; Savage and Crother, 1989), we prefer to regard it and *Urotheca* s.s. as evolutionarily distinct sister genera.

Myers (1974) had erected eight species groups for 45 poorly known snakes of the American mainland between latitudes 35° North and 35° South. Although the monophyly of *Rhadinaea* was not demonstrated, the species groups still seem to represent natural assemblages, which makes it easy to whittle away at the genus. One of the main problems for the future will be to determine which of the remaining species groups form a clade that includes the generic type species, *Rhadinaea vermiculaticeps*.

[4] The nomen nudem "*Caapora*," as cited from labels by Di-Bernardo (op. cit.: 227) was Bailey's unpublished manuscript name.

Central American clade, whereas the two members of the *brevirostris* group examined (*brevirostris* and *occipitalis*) were associated with the South American clade (Cadle, 1984b).

For the above reasons, we find it convenient to resurrect the following available name for Myers' "*Rhadinaea*" *brevirostris* group:

Taeniophallus Cope, 1895

Taeniophallus Cope, 1895: 201, pl. 27, fig. 4 (hemipenis).
Rhadinaea Cope: Myers, 1974 (part: the *brevirostris* group).
Echinanthera Cope: Di-Bernardo, 1992 (part: the *brevirostris* group sensu Myers).

TYPE SPECIES: *Lygophis nicagus* Cope, 1868, is the nominal type species, although, as pointed out by Myers (1974: 17, 208), Cope's original concept and definition of *Taeniophallus* were based primarily on material of the very similar *Rhadinaea brevirostris*.

CONTENT: Seven named species, as follows: *Taeniophallus affinis* (Günther), new combination; *Taeniophallus bilineatus* (Fischer), new combination; *Taeniophallus brevirostris* (W. Peters), new combination; *Taeniophallus nicagus* Cope; *Taeniophallus occipitalis* (Jan), new combination; *Taeniophallus persimilis* (Cope), new combination; *Taeniophallus poecilopogon* (Cope), new combination.

DISTRIBUTION: Lowland South America, from Surinam and Colombia south to northern Argentina (maps 18–20 in Myers, 1974, and maps in Laurent, 1979, and in Di-Bernardo and Lema, 1986, 1987, 1988, 1991).

DEFINITION AND DIAGNOSIS: Small colubrids, usually < 500 mm total length (> 700 mm in *affinis*), lacking hypapophyses on posterior vertebrae; 8–23 prediastemal maxillary teeth + 2 ungrooved fangs, the ultimate offset laterad. *Color pattern:* stripes or anterior spots, most species with either a pale canthal-temporal line or a pale postocular marking. *Scutellation:* ventrals 123–192, paired subcaudals 36–94,[5] anal plate divided; smooth dorsal scales in 17 or 15 rows, with occasional lateral reduction posteriorly to 15 or 13 (respectively); apical pits present or absent, anal ridges absent; supralabials 7 (3–4 touching eye) or 8 (3–5 in eye), only the second touching loreal; subpreocular absent; infralabials 8 or 9 (rarely 7); temporals normally 1 + 2 (2 + 2 also common in *occipitalis*). *Hemipenis:* Single to slightly bilobed; insertion of major retractor muscle slightly divided even when hemipenis is single; unicapitate, or noncapitate; organ proximally spinose, distally calyculate; asulcate side of capitulum modified, bearing enlarged papillae and sometimes spiny knobs or enlarged calyces; sulcus spermaticus single (*nicagus* only) or dividing about mid-organ, with centrolineal branches; no basal nude pocket.

The above combination of traits distinguishes *Taeniophallus* from other genera of snakes. The region of differentiated ornamentation (flaplike papillae, stubby spines, enlarged calyces) on the asulcate side of the hemipenis, although not unique among snakes, is a potential source of synapomorphies for this genus or parts thereof.

DISCUSSION

Myers (1974) defined the *brevirostris* group and provided systematic accounts of the six species included. Owing to the limited material then available, this postulated group of rather diverse species was the least satisfactory of the eight species groups visualized for "*Rhadinaea*." Laurent (1979) amplified knowledge of the Argentine distribution of one species and a recent series of useful papers by Di-Bernardo and Lema (1986, 1987, 1988, 1991) has extended knowledge of four species occurring in eastern and southern Brazil. Di-Bernardo (1992) subsequently submerged the entire "*Rhadinaea*" *brevirostris* group in the same genus with the "*Liophis*" *undulatus* group—in the resurrected genus *Echinanthera*. Indeed, the possibility of close relationship between these groups needs exploring, but, unfortunately, Di-Bernardo (1992) provided little evidence, all it flawed. He misinterpreted (p. 227) the significance of Cadle's (1984a) immunological data, which are ambiguous as to whether the *undulatus* and *brevirostris* groups are closely related other than in the sense of both belonging to the South American xenodontine clade (antisera were not available for any of the several test-

[5] Ranges of ventrals and subcaudals based on combined data from Myers (1974) and Di-Bernardo and Lema (1986, 1987, 1988, 1991).

ed species from these two groups). Furthermore, Di-Bernardo (loc. cit.) claimed that one of the hemipenial characteristics of the *brevirostris* group (enlarged asulcate papillae [Myers, 1974: 35, 195]) "is shared by the taxa '*amoenus*', '*cyanopleurus*', '*melanostigma*' and '*undulatus*'," but his figure 1 of the hemipenis of *Echinanthera cyanopleura* does not show this feature, nor is it present on *Echinanthera* hemipenes examined by us.[6] Despite this claim of similarity, Di-Bernardo on the following page (p. 228) used a different hemipenial character in his diagnosis of *Echinanthera*, which is repeated below in its entirety:

> Xenodontine colubrid (*sensu* Cadle, 1984a) with hemipenis single or slightly bilobate, lacking apical disks and showing a straight middorsal band without ornamentation.

The last character refers to a nude region down the middle of the asulcate stalk of the hemipenis. As noted by Myers (1974: 32),

> Most species [of *Rhadinaea* s.l.] have a nude gap between the spines on the midline of the asulcate side, and in some this nude region takes a characteristic shape and size when the hemipenis is everted.

Contrary to Di-Bernardo's claim (pp. 228–229), this character does not distinguish the *brevirostris* group from other groups of *Rhadinaea*—a nude asulcal gap is not confined to the *brevirostris* group nor is it universal within that group.[7] Therefore, possible relationships between the *brevirostris* group (in whole or in part) and *Echinanthera* have not been demonstrated and remain to be investigated. The availability of the unused generic name *Taeniophallus* prompts us to keep the *brevirostris* group apart for the time being, although the question of the group's monophyly should as a matter of course be challenged and reexamined.

The complex nomenclatural history and provenance of the holotype of *Lygophis nicagus*, nominal type species of *Taeniophallus*, was discussed in detail by Myers (1974: 206–208), who reached the following conclusions:

> . . . the [*Enicognathus*] *melanocephalus* [= Asiatic *Sibynophis subpunctatus*] syntype that Cope (1868, p. 132) later made the holotype of *Lygophis nicagus* looks very much like a specimen of [*Rhadinaea*] *brevirostris*. . . . Dissection of the hemipenis, however, reveals that the specimen is 1) not a *Rhadinaea*, and 2) probably not a South American snake. The hemipenis differs most importantly from *Rhadinaea* and most other xenodontines in having an undivided sulcus spermaticus. . . . although *nicagus* is the nominal type species of *Taeniophallus*, I do not think that it should even be associated with that name . . . Cope's illustration . . . of the hemipenis of "*Taeniophallus nigagus*" seems to be that of a *brevirostris*, and his concept (1895, p. 201) of the monotypic *Taeniophallus* is thus based largely on *Rhadinaea brevirostris* . . .

But the conclusion that the type specimen of *nicagus* probably was not a South American snake is now disproved with discovery in Surinam and Brazil of a *brevirostris*-like snake having a simple sulcus spermaticus (unpubl. data, based on a retracted hemipenis of MCZ 149545 and an everted organ of AMNH 138683).

[6] The papillae on the calyces of everted *Echinanthera* hemipenes in our collections are nearly uniform in size (as suggested in Di-Bernardo's fig. 1) or else increase gradually to become longest near the asulcate edge of the capitulum. In the last case there is no differentiation except for the gradual size increase. Most species of *Taeniophallus* possess some relatively large, compressed (flaplike) papillae on the asulcate side; other species-variable differentiation includes greatly enlarged calyces and thick, knoblike spinules on the asulcate side.

[7] This is not a character observable by dissection of the retracted hemipenis. It is the arrangement of spines *plus differential tissue expansion* that permits a characteristic interspinal asulcal gap to appear upon eversion, as can best be visualized by comparing illustrations of retracted and everted organs of the same species. For example, only a narrow gap is formed upon eversion in "*Rhadinaea*" [*Urotheca*] *lateristriga* (Myers, 1974, fig 4, also fig. 42A,B), whereas a very distinctive gap reminescent of *Echinanthera s.s.* is formed in *Rhadinaea hannsteini* (op. cit., fig. 30D,E). Comparison of everted hemipenes in the aforesaid figures 30 and 42 demonstrates the extreme variability that can exist on the asulcate surface within groups of species. This is said in a cautionary spirit, not to denigrate possible usefulness of the asulcate character in *Echinanthera* sensu stricto.

Everted *Echinanthera* hemipenes prepared by us show a pronounced (broad) interspinal area, on the asulcate side, as indicated by Di-Bernardo. This area is not always nude, however, being broken in some organs by a median row of small spines. The appearance of this area on everted hemipenes of *Taeniophallus* is difficult to predict from descriptions in Myers (1974), who had to rely mainly on dissection of retracted organs. But the arrangement of spines in parallel rows in species as diverse as *T. affinis* and *T. occipitalis* might well show an *Echinanthera*-like gap (nude or with intervening papillae or small spines), but, even so, everted hemipenes of *T. brevirostris* show nothing comparable to the *Echinanthera* condition.

Myers (op. cit.: 202, map 18) had conceived *Rhadinaea brevirostris* as an exceptionally widespread snake, occurring from Colombia to Bolivia along the eastern foot of the Andes and eastward through the Amazon Basin to Pará, Brazil, thence north to French Guiana. Hemipenial and other comparisons of specimens recently collected north of the Amazon, at Serra do Navio in Amapá, extreme northeastern Brazil, show the existence there of typical *brevirostris* (AMNH 138700, 138748) in sympatry with *nicagus* (AMNH 138683). The only eastern specimen from outside of Brazil that was assigned to *brevirostris* by Myers was a female from French Guiana. This specimen and a few eastern Brazilian specimens discussed in Myers have to be reexamined, although the stated Brazilian range of *brevirostris* will remain unchanged; Cunha and Nascimento's (1978: 132–134, pl. 30, fig. 1) description and photograph confirm the existence of *brevirostris* in eastern Pará.

Pending further study, we recognize *Taeniophallus nicagus* as a Guayanan species (from Surinam to at least Amapá, Brazil) distinguished from partially sympatric *T. brevirostris* by the feature of a simple sulcus spermaticus and by certain more accessible differences, including pale dorsolateral blotching on the neck and pale supralabials and genials. *T. brevirostris* has a distinctly divided sulcus, but one of the branches is shorter than the other—such shortening was suggested by Myers (1974: 32–33) as one of the theoretical ways of deriving a simple sulcus from a bifurcate condition, but he did not make the speculative leap that would have allied *nicagus* with the *brevirostris* group.

There seems to be no available generic name for the next group of snakes to be considered.

PSOMOPHIS, NEW GENUS

TYPE SPECIES: *Rhadinaea obtusa* Cope, 1863.

ETYMOLOGY: From the Greek *psomos* (a morsel or bit) + *ophis* (snake), alluding to the minuteness of these snakes, which doubtless are preyed on by many larger animals. Gender masculine.

CONTENT: Three species: *Enicognathus joberti* Sauvage, 1884; *Liophis genimaculata* Boettger, 1885; *Rhadinaea obtusa* Cope, 1863.

DEFINITION AND DIAGNOSIS: Small (≤ 450 mm total length) slender terrestrial colubrids; tail short (16–28% of total length) and stout, terminating in sharp spine; pupil of eye round. *Osteology:* Premaxilla with broad lateral expansions from nasal process, dorsally articulating broadly with nasal bones; about 15–21 prediastemal maxillary teeth + 2 ungrooved fangs, the last slightly offset; no hypapophyses on posterior trunk vertebrae. *Color pattern:* Dark vertebral stripe on paler brown dorsum; lateral dark lines or stripes (sometimes vague) present or side of body uniformly dark. *Scutellation:* High number (> 170) of ventral plates; subcaudals < 90, paired; anal divided. Smooth dorsal scales in 17 or 19 rows at midbody, reducing by loss or fusion of lateral rows to 15 or 17 posteriorly; no apical pits or anal ridges. Supralabials 8, rarely 7, with 2–3 in loreal and 4–5 in orbit; subpreocular absent; infralabials usually 10 (8–11); temporals normally 1 + 2, rarely 1 + 1. *Hemipenis:* Deeply bilobed, bicapitate; lobes acalyculate (pseudocalyculate when retracted)—ornamented on sulcate sides solely with large soft papillae that have minutely spinulate tips, nude on asulcate sides—large spines and spinules present below the lobes; sulcus spermaticus deeply forked, with centrolineal branches; no basal nude pocket.

The above combination of traits distinguishes *Psomophis* from all other Neotropical colubrid genera, very few of which have spiny hemipenes with neither calyces nor apical discs (Myers and McDowell, MS). The configuration of a deeply bilobed, bicapitate hemipenis distally ornamented on the sulcate side solely with enlarged spinulate papillae is unique among colubrids so far as we know.

The high number of ventral scales is unusual in terrestrial (i.e., nonarboreal) Neotropical colubrids, but is approached in some species of *Taeniophallus* (*Rhadinaea* s.l.), which superficially resemble *Psomophis* in habitus and color pattern: *Psomophis genimaculatus* and *P. joberti* will key to *Rhadinaea* in Peters and Orejas-Miranda (1970) and to the species [*Taeniophallus*] *brevirostris* in Myers' (1974) old *Rhadinaea* monograph. *Psomophis obtusus* keys to *Liophis obtusus* using Peters and Orejas-Miranda (1970).

Externally, the number and arrangement of supralabials can be used to key *Psomophis* from *Taeniophallus*: *Psomophis* has eight or rarely seven supralabials, always with numbers 2–3 in contact with the loreal and 4–5 touching the eye; *Taeniophallus* normally has seven or (in *brevirostris* and *occipitalis*) eight supralabials, with only the 2nd touching the loreal and with 3–4 (if seven labials) or 3–5 (if eight) in the orbit. *Psomophis* normally has more infralabials, usually 10 (variation 8–11) vs 8 or 9 in *Taeniophallus*. The posterior reduction in dorsal scale rows further distinguishes *Psomophis* (19 → 17 or 17 → 15) from all *Taeniophallus* except *T. brevirostris* (17 → 15) and occasional *T. occipitalis* (15 → 13).

Species of *Echinanthera* s.s. are easily distinguished from *Psomophis* in being larger snakes with the head relatively distinct from the neck, in having a single, calyculate hemipenis with the sulcus spermaticus dividing more distally, and in having fewer ventrals (< 160), longer tails (28–36% of total length), and more numerous maxillary teeth (> 25).

DISTRIBUTION: Lowland South America east of the Andes, between parallels 0° (mouth of Amazon) and 35°S (Río de La Plata); see figure 1. Except for an isolated record at the mouth of the Amazon (Ilha de Marajó) and upper drainages of southern Amazonian tributaries (Araguaia and Mamoré rivers, in Brazil and Bolivia, respectively), most of the distribution of *Psomophis* lies south and east of the Amazon Basin—in Atlantic drainages of eastern Brazil and in the great drainage system formed by the Paraná, Paraguay, and Uruguay rivers. Most specimens we have seen are from nonrainforest areas (see further under *P. joberti*). Known from Argentina, Bolivia, Brazil, Paraguay, and Uruguay.

DESCRIPTION

Small terrestrial colubrids (≤ 450 mm total length) of slender proportions, with head scarcely wider than neck; body slightly higher than wide; ventrolateral edge of body angulate or rounded depending on species[8]; tail short (17–28% of total length) and stout, terminating in sharp spine; pupil round.

[8] The slight ventrolateral angulation (absent in *P. obtusus*) and the slight lateral compression (all species) is not evident in poorly prepared specimens.

COLOR PATTERN: Light brownish ground color (grayish under stratum corneum), with a median dark stripe on vertebral and adjacent parts of paravertebral rows; median stripe with or without black and/or white edges; one or a few dark lateral lines or stripes, or sides of body overall dark brown. Head darker brown than body or else brown with trace of median stripe to snout; often a discernible dark lateral stripe through eye; a wedge of dark head color extending ventrad behind corner of mouth in two of three species; no distinctive pale canthal or postocular markings; pale nuchal spots or broken collar present or absent. Dark body color encroaching or not onto ends of ventral plates; pale venter otherwise immaculate.

SCUTELLATION: Head plates conform to the normal colubrid pattern. A loreal is present, as are one preocular (but no subpreocular), two postoculars, and usually 1 + 2 temporals (rarely 1 + 1). Upper labials usually 8, rarely 7, with 2–3 always touching the loreal and 4–5 always touching the eye; lower labials usually 10 (range 8–11). Dorsal scales smooth, lacking apical pits and anal ridges, in 19-19-17 or 17-17-15 rows, with lateral reduction. High numbers of ventrals (171–216) and moderate numbers of paired subcaudals (46–83). Anal plate divided.

OSTEOLOGY

DENTITION: Maxilla with moderate number (15–21) of prediastemal teeth, followed by variable diastema and two enlarged, ungrooved fangs, the last being slightly offset laterad (from a plane connecting prediastemal teeth and first fang). Maxillary counts for 41 specimens (generally 1 maxilla per specimen) are tabulated below:

Maxillary teeth	*genimaculatus*	*joberti*	*obtusus*
15 + 2	5	0	0
16 + 2	2	8	1
17 + 2	3	9	2
18 + 2	1	4	3
19 + 2	2	1	2
20 + 2	0	0	0
21 + 2	0	0	1

Teeth also present on palatine, pterygoid, and dentary (see Skull below).

SKULL: A skull of *Psomophis joberti*

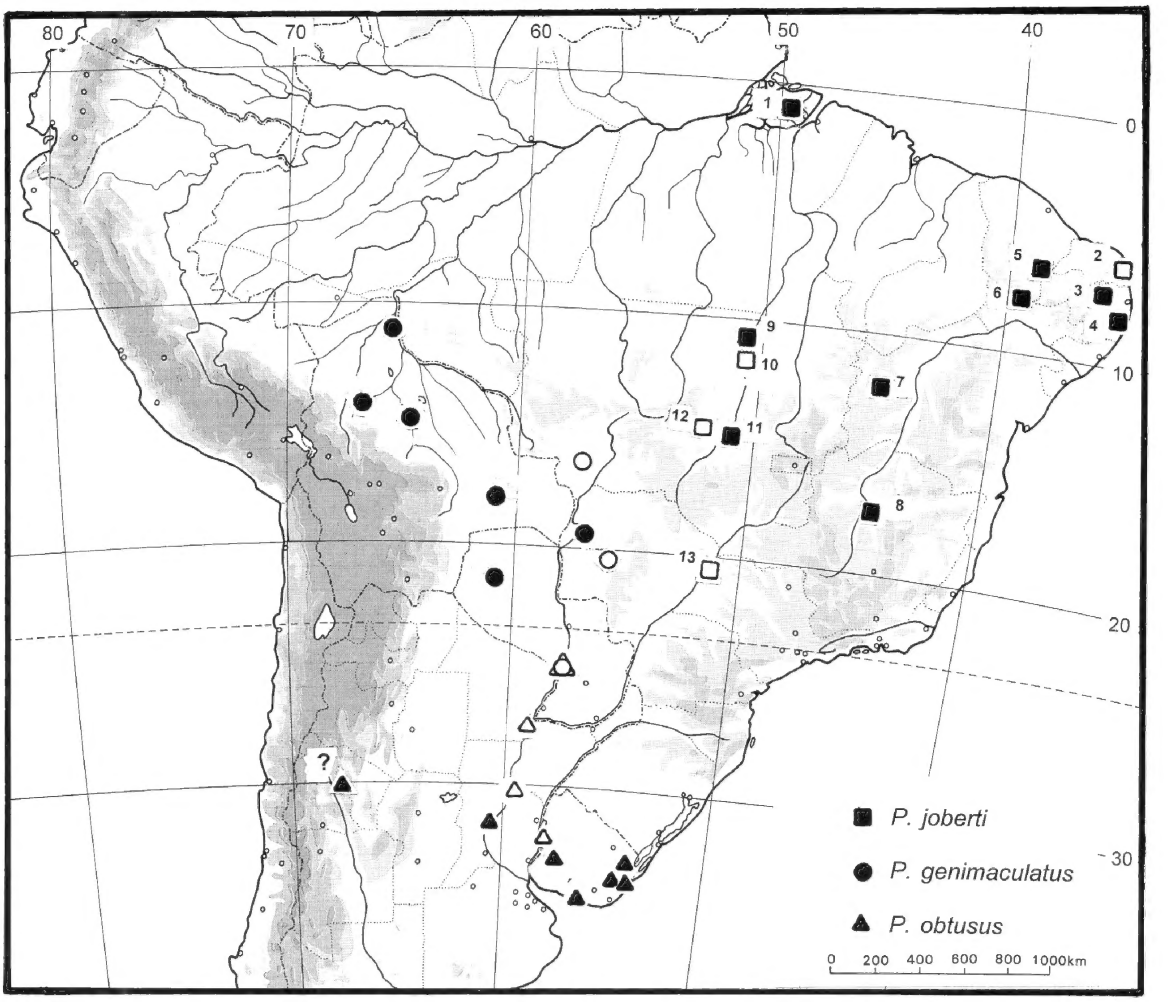

Fig. 1. Distribution of the species of *Psomophis*, new genus. Solid symbols denote specimens examined; open symbols are literature records, including a few instances of inferred identity as indicated in the text and appendix. Numbers refer to *Psomophis joberti* localities, which are referenced to major habitats in the text (see pages 22–23, 29). A few symbols represent multiple contiguous localities. See text regarding questioned locality for *P. obtusus* in western Argentina.

(AMNH 87960) was cleared and stained, and the mandibles and the palatomaxillary arches removed, for the following description and illustration (fig. 2). Tooth counts (left/right) for this specimen are, maxillary (16 + 2/17 + 2), palatine (14/12), pterygoid (29/28), dentary (28/26). The pterygoids are toothed to the point where they flare laterally toward the quadrates.

Paired frontals longer than broad, widely separated dorsally from nasal plates. The postorbitals are curved struts, narrowly separated from frontals by a parietal flange. Posterior edge of parietal broadly rounded, with a small point projecting posteriorly at midline. Supratemporal bones short, not in contact with parietal and barely projecting onto exoccipitals. Premaxilla, in anterior and dorsal view, with broad lateral expansions (nasal laminae) of nasal process that dorsally articulate broadly with the dorsal plates of nasal bones (see Discussion for expanded description of premaxilla). Dorsal plates of nasals emarginated anterolaterally and posterolaterally. Quadrates roughly triangular, with broad base dorsally. In lateral view, prefron-

tals are a more or less vertical plate with a slightly bulging midportion. As is typical for most small snakes, ridges and crests for muscle attachment are lacking in *Psomophis joberti;* the dorsal and ventral surfaces of the skull, including parietal, supraoccipital, exoccipitals, and sphenoid are smoothly rounded.

Orbital fenestra large, with emargination of parietal and frontals, its ventral border composed of a very large frontal crest on the sphenoid. Frontal sits very high above trabecular grooves on this crest. At posterior intersection of frontal with the frontal crest of the sphenoid, the ventral extension of the frontal is about ⅔ the vertical dimension from top of skull to ventral border of sphenoid. Hence, the frontal and parietal are widely separated below the orbital foramen. Trabecular groove open along entire length, with a small perforation in one portion. Sphenoid with small suborbital flanges, and a long cultriform process extending well anterior to nasal processes of palatine; anterior end of cultriform process concave and slightly flared; cultriform process bearing a broad deep groove ventrally.

Vidian canals rather long and symmetrical; their posterior orifices at posterolateral edge of sphenoid; their anterior orifices barely within the sphenoid margin, somewhat behind posterior border of the suborbital flange.[9] Trigeminal foramina double on each side, separated by broad flange of prootic. Ventral to each trigeminal foramen on each side is a pair of sympathetic foramina.

VERTEBRAE: No hypapophyses on posterior trunk vertebrae.

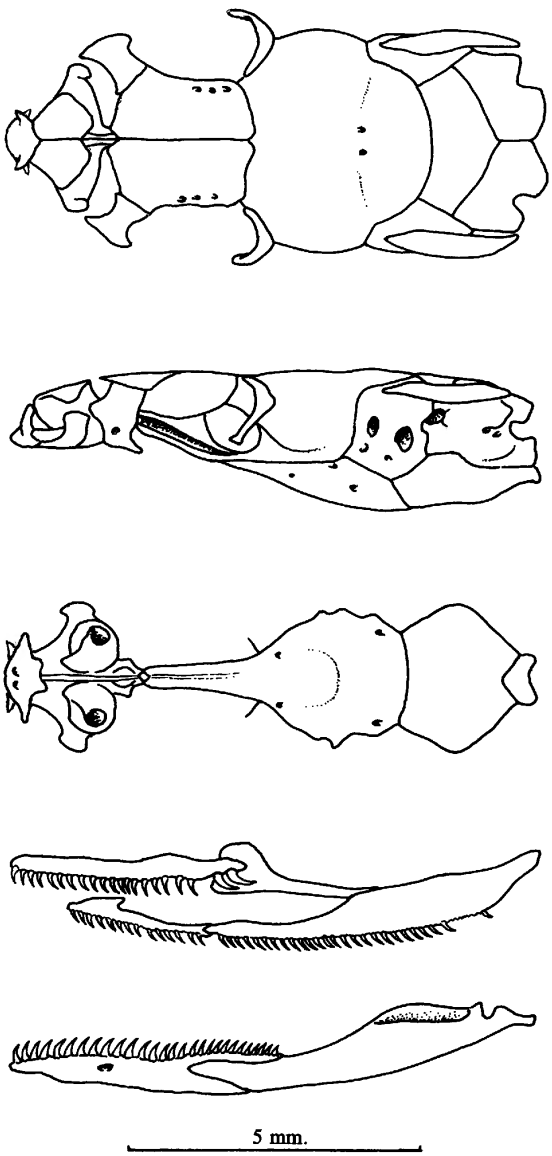

Fig. 2. Skull of *Psomophis joberti* (AMNH 87960).

HEMIPENES

The first description below is of the everted organ of *P. genimaculatus*, the only species for which we have seen an inflated hemipenis; this is followed by descriptions of a retracted organ each for *genimaculatus*, *joberti*, and *obtusus*. When comparing everted and retracted hemipenes, it should be remembered that the apex of the former is not necessarily equivalent to the apex of the latter, as is often indicated by differing points of termination of the branches of the sulcus spermaticus (Myers, 1974: 33). The everted organ is oriented mainly by reference to its sulcate and asulcate sides. Retracted organs, whether left or right, additionally can be usefully oriented

[9] The anterior foramen in *Psomophis joberti* is most likely a secondary foramen providing outlet for the palatine nerve and an accompanying sympathetic nerve from the cranial cavity. The primary anterior Vidian foramen, which lies within the braincase in most colubrids, cannot be seen without disarticulated skulls. See Underwood (1967: 15–18) for a discussion of some pertinent aspects of the morphology of the Vidian canal in colubrids.

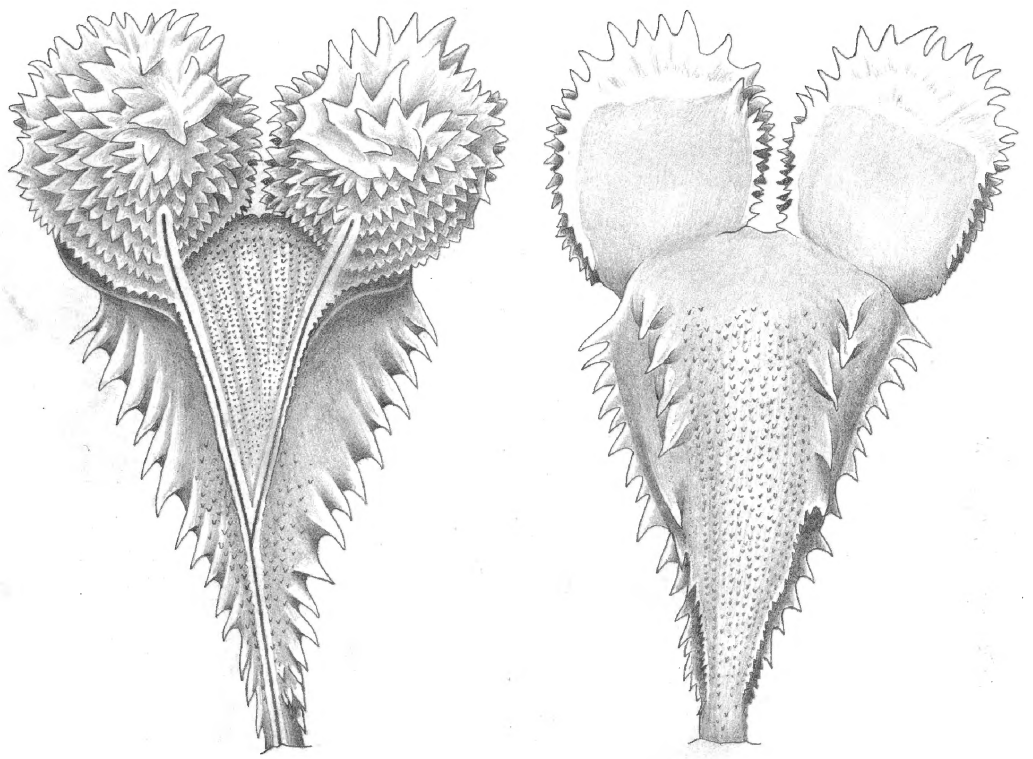

Fig. 3. Hemipenis of *Psomophis genimaculatus*. Fully everted left organ of USNM 331437, shown in sulcate (left) and asulcate (right) views; approximately ×3.6.

by reference to their ventral and dorsal, and lateral and medial walls.

***Psomophis genimaculatus* (everted)**: The hemipenes of one adult specimen (USNM 331437) were fully everted during preservation. The left organ was removed and inflated with colored petroleum jelly for description and illustration (fig. 3). This organ, which extended to about the 11th subcaudal before removal, is about 15 mm long (strong curvature prevents accurate determination).

The hemipenis is about one-third bilobed, becoming widely expanded distally from a very narrow base. The sulcus spermaticus is deeply forked, dividing about 4 mm from the base, each fork extending about halfway up the middle of each lobe in centrolineal orientation. The sulcate surface of each lobe of the everted hemipenis bears a dense array of large papillae, many of which appear relatively blunt in gross aspect but which can be seen under high magnification (and with proper lighting) to have minutely spinulate tips. These spinulate papillae (or soft spines) arrayed in rows slightly oblique to either side of a branch of the sulcus spermaticus, with papillae in each row being loosely connected along their bases. Calyces are absent.

The papillate sulcate side of each lobe is independently delimited by a broad free-hanging edge. Except where interrupted by a branch of the sulcus spermaticus, this overhang is complete proximally and around the sides of the lobe, but distally it greatly lengthens and straightens—so that the extended "underside" of the overhang becomes a broad flap (not inflatable, apparently solid), which, at its broadest, comprises about a third the width of the lobe, as visualized from the asulcate side. The distal flap is fringed with spinulate papillae projecting from the sulcate side.

The asulcate sides of the lobes, including distal flap, are completely smooth and unornamented (nude). On the asulcate side, each lobe is incompletely delimited from the body

of the organ by a shallow groove extending about halfway around the base of the lobe.

The body or stalk of the hemipenis is spinose in a definite pattern. Each side of the sulcate surface bears a series of about 15–17 moderate-size, nearly straight spines, gradually decreasing in size proximally, where the two rows converge on either side of the undivided part of the sulcus spermaticus. The sulcate surface between these rows is covered with minute spinules[10] both inside and outside the fork of the sulcus spermaticus, this ornamentation becoming sparse in the crotch of the organ. Extending proximally from each lobe, the free-hanging edge of the capitulum approaches the branch of the sulcus spermaticus, then extends proximally along the outer edge of the branch for about a fourth to a third the distance to the base of the organ. The overhang adjacent to the sulcus and at the base of the lobes is bordered by a row of enlarged spinules.

On the asulcate side, a line of five moderate-size spines is positioned laterally below each lobe. The "side" of the organ between these spines and those fringing the sulcate surface is nude. Otherwise the entire asulcate surface of the stalk is spinulate nearly to the base of the nude lobes.

***Psomophis genimaculatus* (retracted)**: The uneverted right hemipenis of CM 34853 was examined in situ and a previous incision was completed roughly along its midventral surface, the organ being then removed and pinned out for detailed study. The retracted organ bifurcates at the middle of subcaudal 9, with the two long lobes extending to the middle of subcaudal 13. The two divisions of the major retractor muscle merge at the base of subcaudal 15 and the muscle originates far posteriorly at the level of subcaudal 41 (18 subcaudals from the tail tip).

The lobes comprise 30 percent of the organ's total length. The sulcus spermaticus forks proximally, 30 percent from the base (less than halfway up the basal stalk), with one long branch extending virtually to the tip of the ventral lobe and the other branch extending similarly in the dorsal lobe (opened by incision along medial side). Each sulcus branch extends along the lateral side of its lobe and the orientation is therefore centrolineal (as in the everted organ).

The sulcate side of the lobe is covered with large papillae, all of which terminate in minute, slightly recurved spinules. The papillae are vaguely arranged in oblique rows; in places, the unexpanded, interrconnected tissue at the bases of the papillae gives a false impression of calyces. The asulcate side of the lobe (i.e., the dorsal wall of the retracted ventral lobe and the ventral wall of the retracted dorsal lobe) is a completely nude area of longitudinally folded, thin, translucent tissue. This tissue forms to each side a pronounced wall (the "capitate overhang") separating the papillate and the nude areas of the lobe; the wall is continuous from one side to the other around the end of the organ, where the papillate tip of the lobe forms a a deep overhang over the nude area.

The stalk of the organ below the lobes is spinulate overall, with four definite rows of moderate-size, barely recurved spines. Two of the rows each contain over a dozen spines and converge proximally on either side of the sulcus spermaticus. Each of these long rows nearly connects distally with a shorter, parallel row of six spines high on the stalk; these last rows flank a broad, median asulcate gap. (Each of the shorter rows of spines will lie laterally below the nude asulcate side of a lobe; see fig. 3.)

***Psomophis joberti* (retracted)**: The uneverted left hemipenis of MZUSP 4406 was examined in situ and opened along its midventral surface, the organ being then removed and pinned out for study. The retracted organ bifurcates at the end of subcaudal 11, with the two long lobes extending to the end of subcaudal 15. The two divisions of the major retractor muscle merge at the end of subcaudal 18 and the muscle originates far posteriorly at the level of subcaudal 44 (23 subcaudals from the tail tip).

The lobes comprise 33 percent of the organ's total length. The sulcus spermaticus forks proximally, 29 percent from the base (less than halfway up the basal stalk), with one long branch extending virtually to the tip of the ventral lobe and the other branch extending similarly in the dorsal lobe (opened

[10] These exceptionally small spinules might be interpreted as pointed (spinelike) papillae, but, under proper lighting, they have the appearance of being mineralized.

by incision along medial side). Each sulcus branch extends along the lateral side of its lobe and the orientation is therefore centrolineal (as in the everted organ).

The sulcate side of the lobe is covered with large, soft papillae, which terminate in minute, slightly recurved spinules. The papillae are vaguely arranged in oblique rows to either side of the sulcus branch; the interconnecting, unexpanded tissue at the bases of the papillae gives a false impression of calyces. The asulcate side of the lobe (i.e., the dorsal wall of the retracted ventral lobe and the ventral wall of the retracted dorsal lobe) is a completely nude area of longitudinally folded, thin, translucent tissue. This tissue forms to each side a pronounced wall (the "capitate overhang") separating the papillate and the nude areas of the lobe; the wall is continuous from one side to the other around the end of the organ, where the papillate tip of the lobe forms a a deep overhang over the nude area. In both the dorsal and ventral lobes, a single spine is interspersed with the spinulate papillae about midway along one edge of the capitate overhang; this spine is very slightly larger than immediately adjacent papillae but is no larger than the largest papillae.

The stalk of the organ below the lobes is spinulate overall, with four definite rows of moderate-size, barely recurved spines. Two of the rows each contain over a dozen spines and converge proximally on either side of the sulcus spermaticus. Each of these rows connects distally with a shorter, parallel row of five or six spines high on the stalk (i.e., on its distal third); these last rows flank a broad, median asulcate gap.

***Psomophis obtusus* (retracted)**: The uneverted left hemipenis of BMNH 1901.3.2.2 was examined in situ and opened along its midventral surface, then removed and pinned out for detailed study. The retracted organ bifurcates at the end of subcaudal 8, with the two long lobes extending to the end of subcaudal 13. The two divisions of the major retractor muscle merge at the end of subcaudal 16 and the muscle originates posteriorly at about the level of subcaudal 36 (28 subcaudals from the tail tip).

The lobes comprise 40 percent of the organ's total length. The sulcus spermaticus forks proximally, in the basal third of the organ (about halfway up the basal stalk), with one long branch extending nearly to the tip of the ventral lobe and the other branch extending similarly in the dorsal lobe. Each sulcus branch extends along the lateral side of its lobe and the orientation is therefore centrolineal.

The sulcate side of the lobe is covered with large papillae bearing minute, recurved spinules on their tips; the unexpanded, interconnected tissue at the bases of the papillae gives a false impression of calyces. The asulcate side of the lobe is completely nude except for a short vertical line of four spinulate papillae just above the base of the lobe. There is a pronounced wall (the "capitate overhang") separating the papillate and the nude areas of the lobe; the wall is continuous from one side to the other around the end of the organ, where the papillate tip of the lobe forms a a deep overhang over the nude area.

The sulcate side of the stalk bears small papillae within the fork of the sulcus and spines to either side of the fork. Proximally, the sulcus spermaticus is flanked by small recurved spines from the base of the organ to slightly past the point at which the sulcus forks. The distal half of the stalk—on the sulcate side—is densely covered with about 30 moderate-size, slightly recurved spines which are not arranged in definite rows but which terminate abruptly along each side of a broad, median asulcate gap. The asulcate gap is spinulate to the bases of the lobes. The basal half of the stalk is spinulate overall except for the spiny sulcus border.

Discussion

Based on the above descriptions, we here examine in greater detail the unique hemipenes and premaxillae of *Psomophis* and make the generalizations that seem to us obvious or pertinent.

Unusual Hemipenes

Based on a small sample size of only one or two organs per species, the hemipenes of *Psomophis* species show relatively few differences. The organs of *P. genimaculatus* and *P. joberti* seem nearly identical in general physiognomy, including relative length of lobes and arrangement of spines in four definite longitudinal rows below the lobes. The one hemipenis examined of *joberti* differed

curiously from two *genimaculatus* organs in having, on one edge of each capitulum, a single spine among the spinulate papillae. The retracted hemipenis of *P. obtusus* is rather similar to those of the other species (and probably is similarly shaped upon eversion), with two main differences: the lobes are longer in *obtusus*, comprising 40 percent of hemipenial length (vs. 30–33%); the spines below the lobes are not arranged in definite rows in *obtusus* but rather are clustered on the midsection of the asulcate side.

Any particular type of hemipenis cannot be fully comprehended without study of both its retracted and its everted conditions. In the case of *Psomophis*, certain features in each state would have been missed or misinterpreted if only one or the other had been studied. The hemipenes of species in this genus are highly unusual in several respects: (1) presence of large, spinulate papillae (soft spines) on the lobes, (2) a false impression of calyces (pseudocalyculation) when in the retracted condition, (3) bicapitation with a centrolineal (vs centripetal or centrifugal) sulcus spermaticus, and (4) an upturned flap bordering the distal "asulcate" edge of each capitulum of the everted organ (in *P. genimaculatus* and probably also in the other two species, based on similarity of retracted organs).

1. Spinulate Papillae (Soft Spines): Papillae as large as those on the lobes of adult *Psomophis* hemipenes are unusual and we have not previously noticed any that terminated in mineralized spinules. The minute spinulate tips suggest the possibility that these structures are actually spines in which mineralization (an ontogenetic event) has been almost entirely arrested. Consistent with this idea are two other observations: Each capitulum of the one *P. joberti* hemipenis examined bears a single, indisputable hard spine that is approximately the same size as surrounding "papillae." Some of the large distalmost "papillae" seem subtly stiffer than others when micromanipulated, suggestive of weak mineralization. The phylogenetic inference to be drawn is that the hemipenis of *Psomophis* is derived from one that was distally spinose.

2. Pseudocalyculation: Most xenodontines have the distal end(s) of the hemipenis surfaced with a reticulum of tissue ridges forming little cups or *calyces*. This pattern is equally present and discernible both on everted organs and in dissected retracted ones, although calyculation may be largely concealed by an abundance of usually small papillae or spinules rising from atop the calyx walls. Retracted *Psomophis* hemipenes appear to be calyculate with exceptionally large papillae, but the papillate surfaces are acalyculate on the everted hemipenis! Closer inspection leads to the conclusion that the inverted organs bear *false* calyces—a kind of structure of which we were heretofore unaware.

The pseudocalyces in *Psomophis* are formed from expansible, interconnected folds of tissue connecting the bases of the spinulate papillae. The resemblance to calyces is striking, particularly when the inverted lobe is incised and gently parted, but the interconnected ridges can be flattened by micromanipulation with fine teasing needles and the cross connections disappear when the hemipenis is fully everted. The organ shown in figure 3 had but weak indications of tissue folds connecting single rows of spinulate papillae.

Although we cannot disprove possibilities that these structures are either primitive or vestigial calyces, we suspect that they simply represent a method of folding expansible tissue when the *Psomophis* hemipenis is inverted for storage.

3. Bicapitation and Orientation of the Sulcus Spermaticus:[11] In sulcate view, the evert-

[11] Hemipenial terminology follows Myers (1973, 1974) and Myers and Campbell (1981: 15), except that the term *pseudocalyculate* is new. Regarding presence or absence and degree of capitation, the terms *noncapitate*, *unicapitate*, and *bicapitate* are nearly self-explanatory, but *semicapitate* is not.

"Semicapitate" can apply to undivided hemipenes having an abbreviated overhang (e.g., one confined to the asulcate tip), but the term usually has been applied to distinctly lobed organs that are somewhat intermediate between the unicapitate and bicapitate conditions. Whether or not calyces flow continuously from one lobe to the other, these organs are too deeply divided for there to be a single head region. Myers (1973: 31) stated that "if capitation is present, it is manifest in a separate overhang below the asulcate tip of each lobe." The overhang actually may be continuous from one lobe to another and extend laterally to the sides of the organ; even so, the organ appears almost two-headed but without complete, separate capitation on each lobe.

ed hemipenis of *Psomophis genimaculatus* is perceived as bicapitate, that is, to have a separate head on each lobe, even though the overhang that defines normal capitation appears to have been greatly modified, by development of a flap (see "4" below) at the distal asulcate edge of each lobe when everted. The inverted hemipenes of *P. joberti* and *P. obtusus* have capitate overhangs as pronounced as in the inverted *genimaculatus* hemipenis and bicapitation therefore seems equally well developed in all three species.

Although not particularly common, bicapitation has been derived more than once, as suggested by variation in orientation of the two heads and the correspondingly differing courses of the branches of the sulci spermatici. In *Psomophis*, the two heads "face" the same way and the sulcus spermaticus has a centrolineal orientation—that is, the sulcus branches diverge moderately to lie on the same side of the hemipenis as the fork, which can be determined by examination of everted organs and by dissection of retracted ones (Myers and Campbell, 1981: 16–17). Examples of other, contrasting conditions among xenodontines with bicapitate hemipenes are: (1) The tribe Pseudoboini Bailey, 1967, in which the heads tend to "turn away" from each other and the sulcus branches consequently curve centrifugally to the outer side of each lobe (see Jenner and Dowling, 1985: fig. 2; Zaher and Caramaschi, 1992: figs. 1–3, 5); (2) The genus *Tantalophis*, in which the everted heads turn to "face" one another and the sulcus branches consequently diverge minimally to lie on adjacent sides of the lobes in centripetal orientation (Myers and Campbell, 1981: figs. 11–12).

4. Asulcate Flap (Everted Organ): Part of the distal ornamentation of each capitulum of an everted hemipenis (whether uni- or bicapitate) commonly is visible from several perspectives. In the everted *Psomophis genimaculatus* organ, however, the disal overhang is so exceptionally flexed toward the sulcate side that only the edge of the overhang is visible in asulcate view (see fig. 3). Although it is not uncommon for the free overhang that defines the capitulum to be interrupted on or near the asulcate midline (e.g., by fusion with the stalk below), the asulcate upward turning of this structure on the separate heads of the everted *Psomophis genimaculatus* hemipenis is quite unusual. Nonetheless, the flap forms a seemingly normal albeit exceptionally deep capitate overhang when the organ is retracted, in which state the potental upturning cannot be predicted. It would be interesting to know whether the distal flap would upturn and whether flexing would be so pronounced if the major retractor muscle were severed prior to eversion.

When morphological variation is extensive across taxa, such terms as bicapitate and semicapitate, centrolineal and centrifugal, etc. become general descriptors, not necessarily implicit statements of homology or even of overall resemblance. In general physiognomy, for example, the bicapitate hemipenis of *Psomophis* appears no more similar (perhaps less so) to the bicapitate organs of pseudoboines than to the semicapitate organ of *Saphenophis* (AMNH 129609, everted).[12]

A Premaxillary Modification

The cleared and stained skull of *Psomophis joberti* described above is unusual among colubrids in the form of the premaxillary bone (fig. 4). In anterior and dorsal view, the body (nasal process) of the premaxilla bears expanded lateral laminae (hereafter referred to as *nasal laminae*). As the laminae project laterally they also curve somewhat anteriorly

[12] Jenner and Dowling (1985) misinterpreted published figures of the hemipenes of *Saphenophis* and *Tropidodryas* as being bicapitate with centrifugal sulci spermatici and, solely on that basis, placed both genera within Bailey's (1967) Pseudoboini. However, neither genus has a bicapitate hemipenis: *Saphenophis* has a semicapitate hemipenis with a centrolineal sulcus spermaticus. *Tropidodryas* does have a centrifugal sulcus, the branches of which pass to the outer, calyculate sides of the lobes, but the calyculate areas are not set off by an overhang and the lobes are therefore noncapitate.

Although Jenner and Dowling (1985: 170–171) noted that immunological studies (Cadle, 1984a, 1984b) corroborated several of their conclusions concerning xenodontines (s.l.) in general, and pseudoboines in particular, they failed to point out that those same data (Cadle, 1984a: 15–16) failed to show any relationship between *Tropidodryas* and the pseudoboines. Because immunological data and/or hemipenial structure refute an association between either *Tropidodryas* or *Saphenophis* and the pseudoboines, the latter group is here considered in its original formulation (Bailey, 1940), as modified by Bailey (1967).

away from the nasal process, thus making the anterior surface of the premaxilla slightly concave. Dorsally, the laminae make a broad contact with the nasal bones along the entire anterior edge of the nasals. Thus, there is a more or less vertical bony plate (thin, but well-ossified) at the tip of the snout.

In ventral view the premaxilla is broadly rounded anteriorly, with the anterior edges of the ventral plate sloping gently laterally and posteriorly to form thick, acutely pointed ventrolateral projections toward the maxillae. Posteromedially from the body of the ventral premaxillary surface projects a bilobed process, the lobes bluntly rounded and separated by a shallow indentation; this process is closely appressed to the septomaxillae.

In lateral view the medial ventral portion of the premaxilla is bluntly pointed and projects slightly anteriorly.

After observing the unusual form of the premaxilla in *Psomophis joberti*, we dissected a specimen of each of the other two species, *P. genimaculatus* (USNM 331437) and *P. obtusus* (CM 55413). The skin of the snout region of each specimen was peeled back and the premaxilla examined in situ. Both specimens have the unusual lateral laminae projecting from the nasal process, a concave anterior surface of the bone, and broad nasal-premaxilla contact. Moreover, in both these specimens, the concave anterior surface of the premaxilla was filled with a tough pad of connective tissue. Although subtle, and subject to a limited sample size, the nasal laminae in the specimen of *P. obtusus* seemed somewhat less developed (narrower) than in the other two species, despite it being the largest of the three specimens.

Bogert (1947: 11) called attention to the potential systematic significance of premaxillary shape in colubrids: "this element of the skull can profitably be used in defining genera or in working out phylogenies." Bogert, however, concentrated his discussion almost exclusively on premaxillary shape as revealed in ventral view, and with particular reference to burrowing taxa. Bogert's work notwithstanding (see also Underwood, 1967: 18–19), characters of the premaxilla have not been routinely employed in colubrid systematics, despite considerable variation in this bone.

In agreement with Bogert's assessment, the

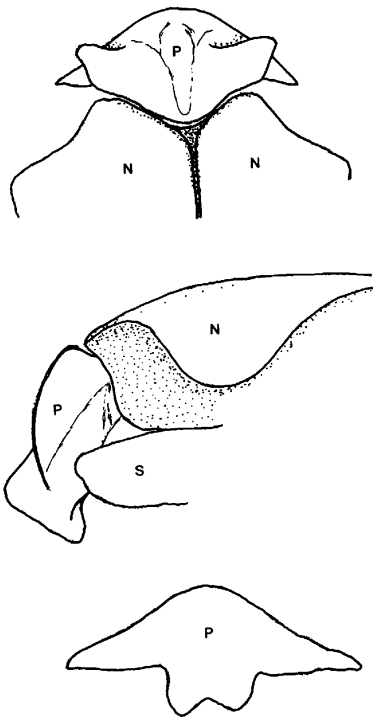

Fig. 4. Premaxilla of *Psomophis joberti* (AMNH 87960) in dorsal, lateral, and ventral view. *Abbreviations:* P, premaxilla; N, nasals; S, septomaxilla.

shape of the premaxilla provides support for the monophyly of *Psomophis*. Although we have not undertaken a systematic survey of variation in premaxillary shape among colubrids, we have casually surveyed the form of this bone in connection with other work on Neotropical colubrids, but have seen no other snakes with the laterally flaring nasal laminae of *Psomophis*. In most South American xenodontines, the premaxilla shows the characteristic form that might be considered "typical" of generalized colubrids: in anterior view, the nasal process is a narrow, often spikelike process which only narrowly contacts the dorsal plates of the nasal bones at their anteromedial juncture. However, many colubrids, particularly those known or suspected to be burrowers, show modifications of the premaxilla similar in general form to that of *Psomophis* (see Bogert, 1947: 11—13 for discussion of some of this variation). These general features include the broadened anterior plate of the premaxillary nasal process, and broad contact between the premaxilla and the dorsal plate of the nasal bones. A

brief comparison of readily accessible skulls of some South American colubrids with such modified premaxillae suggests to us that all the surveyed taxa differ in detail from the modifications observed in *Psomophis*, which are quite similar among the three species. Thus, although we call attention to the modified premaxilla as an autapomorphy of *Psomophis*, statements concerning any broader phylogenetic significance must be deferred until variation in premaxillary form is better understood.[13]

The strengthened premaxilla in *Psomphis* and occurrence of similar modifications in other snakes known to be burrowers suggest to us that *Psomophis* has burrowing proclivities to some degree. This seems supported also by the indistinct neck and by the relatively short, stout, sharply pointed tail. This inference is difficult to reconcile only with Strussmann and Sazima's tabulation (1993: 161) of one species of *Psomophis* as being semiarboreal (see *P. genimaculatus*, Natural History).

SYNOPSES OF SPECIES

KEY TO SPECIES

1. Dorsal scales in 19 rows at midbody, reducing to 17 rows posteriorly; posterior sides of body and ventral tips dark pigmented (fig. 9) ... . *Psomophis obtusus*
   Dorsals in 17 rows, reducing to 15; dark lateral lines or stripes indicated at least vaguely, ventral tips weakly pigmented at most .. 2
2. Dark wedge of head color extending ventrally and curving around angle of jaws (fig. 5A) *Psomophis genimaculatus*
   No conspicuous dark wedge behind corner of mouth, pale color of supralabials continuous with that of pale infralabials (figs. 5B, 10A,B) ..... *Psomophis joberti*

[13] Neotropical colubrids showing similar tendencies in form of the premaxilla comprise members of two major clades and at least several subclades within those. The following list is intended only to indicate the diverse array of South American snakes with such modified premaxillae and is not exhaustive: Colubrines: *Simophis rhinostoma* (MCZ 20753) and *Stenorrhina degenhardtii* (FMNH 232576). Xenodontines: Xenodontini (sensu Myers, 1986): *Lystrophis dorbignyi* (FMNH 9508, FMNH 10199, MCZ 20745), *L. semicinctus* (FMNH 10863). Pseudoboini (sensu Bailey, 1967): *Phimophis guianensis* (FMNH 22579), *Pseudoboa haasi* (MCZ 20802) *P. nigra* (UMMZ 149963), *Rhachidelus brazilii* (MCZ 21671). Other South American Xenodontines (sensu Cadle, 1984a, 1984b): *Apostolepis quinquelineata* (Savitzky, 1978: 75), *Elapomorphus quinquelineatus* (MCZ 20768, 20663). No similarly modified premaxillae have been noted in *Liophis* or *Rhadinaea*.

Psomophis genimaculatus (Boettger), new combination

Figures 3, 5A, 6

Dromicus lineatus (Linnaeus): Duméril et al. 1854: 655, part (specimens mentioned on p. 656 from Santa Cruz, as suggested by Boettger, 1885a: 229).

Liophis (Lygophis) genimaculata Boettger, 1885a: 229–231 (type locality, Paraguay).

Rhadinaea genimaculata (Boettger): Boulenger, 1894a: 170; 1894b: 347; 1896: 635.

Liophis joberti (Sauvage), part: Hoge, 1958: 223. Peters and Orejas-Miranda, 1970: 178.

LECTOTYPE: BMNH 1946.1.5.83, designated by Hoge (1958: 222), who inadvertently transposed the last two numerals. The lectotype (figs. 5A, 6) is a male in good condition, 362 mm total length, 72 mm tail length, with 190 ventrals (excluding 1 preventral) and 54 pairs of subcaudals. This particular specimen also is recognizable by presence of a small azygous scale between the anterior tips of the first genials (just behind the common suture of the first pair of infralabials) and by a former injury that left misshapen lateral scales and ventral plates on the left side (between ventrals 55 and 61).

DIAGNOSIS: *Psomophis genimaculatus* is similar to *P. joberti* in scutellation but is separable by details of color pattern, especially at the angle of the jaws: In *P. genimaculatus* the pale color of the supralabials is separated from that of the throat and infralabials by an anteroventrad curvature of part of the dark brown temporal stripe around the corner of the mouth. *Psomophis obtusus* also usually has a dark wedge of color behind the mouth but it does not extend anteriorad, and *obtusus* is distinguished also by its dark sides and 19 scale rows.

The unrelated *Taeniophallus poecilopogon* has an anteriorly curving wedge of dark color behind the mouth very similar to that in *Psomophis genimaculatus* (compare fig. 5A with fig. 45B in Myers, 1974), but *T. poecilopogon* is readily identified by such features as a vivid

pale canthal-postocular line, dark sides, variably dark speckled or spotted supralabials and throat, and lack of scale-row reduction.

DISTRIBUTION: Eastern Bolivia and the Pantanal of southwestern Brazil, south through the Chaco of northern Paraguay to at least Asunción and possibly to northern Argentina (see Remarks).

DESCRIPTION: Largest specimen a female 451 mm total length, 78 mm tail length; largest male 407 mm total, 85 mm tail. Tail 17–24 percent of total length (17–19% ♀, 20–24% ♂). Ventrolateral edges of body weakly angulate. Dorsal scales in 17-17-15 rows, with reduction occurring by loss of row 4 or fusion of 3 + 4. Ventrals 189–213, highest in females (8♂ 189–203, $\bar{x} = 195.5 \pm 5.01$; 5♀ 195–213, $\bar{x} = 206.1 \pm 9.52$). Subcaudals 46–70, much highest in males (7♂ 54–67, $\bar{x} = 62.7 \pm 4.79$; 5♀ 46–55, $\bar{x} = 52.0 \pm 3.46$). One preocular, two postoculars, 1 + 2 temporals, eight or rarely seven supralabials (2–3 in loreal, 4–5 in orbit), usually 10 (9–11) infralabials.

Pale brownish body with three usually vivid, narrow, darker stripes, including a dark brown median stripe (vertebral and edges of paravertebral rows). The median stripe tends to have dark edges, which usually are further emphasized by an adjacent narrow white line or series of white dashes. Top of head uniformly colored or with tan mottling sometimes outlining a vague cephalic extension of median body stripe, which otherwise starts at rear of head and fades toward end of tail. Top and upper sides of head overall darker than body (i.e., a dark head cap)—or brown on top and blackish brown on sides, the darker color forming a lateral stripe extending from tip of snout through eye and continuing to side of neck. A ventrad extension of the dark head cap or lateral head stripe crosses last supralabial and curves anteriorly around angle of mouth onto last few infralabials, isolating pale supralabial area from the pale color of throat and underside of head. A tendency for a broken pale nuchal collar 1-scale wide from throat to middorsal stripe; pale collar sometimes further broken by lateral dark stripe, isolating a pair of ill-defined pale nuchal spots behind the dark head.

A brown lateral stripe anteriorly on row 4 or adjacent parts of rows 3–4 or 4–5, posteriorly on adjacent parts of rows 3–4 or 4. Lateral stripe black-edged in some specimens, vague on anterior half of body in one specimen; lateral body stripe continuous or not with lateral head stripe and extending sharply nearly to tail tip. Several specimens have a less distinct set of vague stripes or dashes on row 1 or rows 2–3.

Tips of ventrals and subcaudals may be weakly speckled with dark but ventral surfaces otherwise immaculate. A vague orangish wash posteriorly on venter of a recently

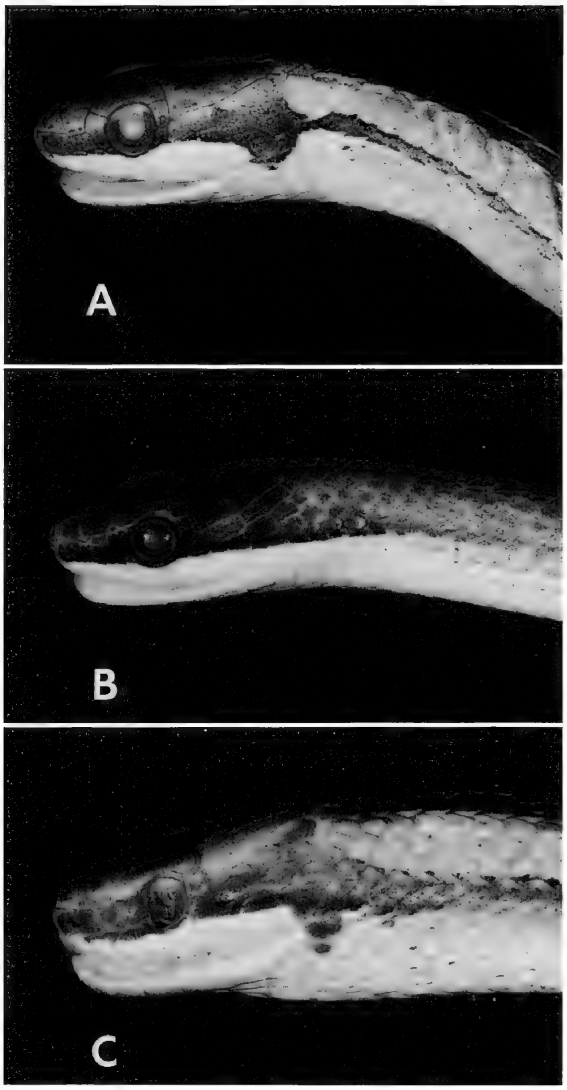

Fig. 5. Heads of the three species of *Psomophis*, in lateral view, ×3.5. **A.** *P. genimaculatus* (BMNH 1946.1.5.83, lectotype). **B.** *P. joberti* (MZUSP 4335). **C.** *P. obtusus* (CM 55413).

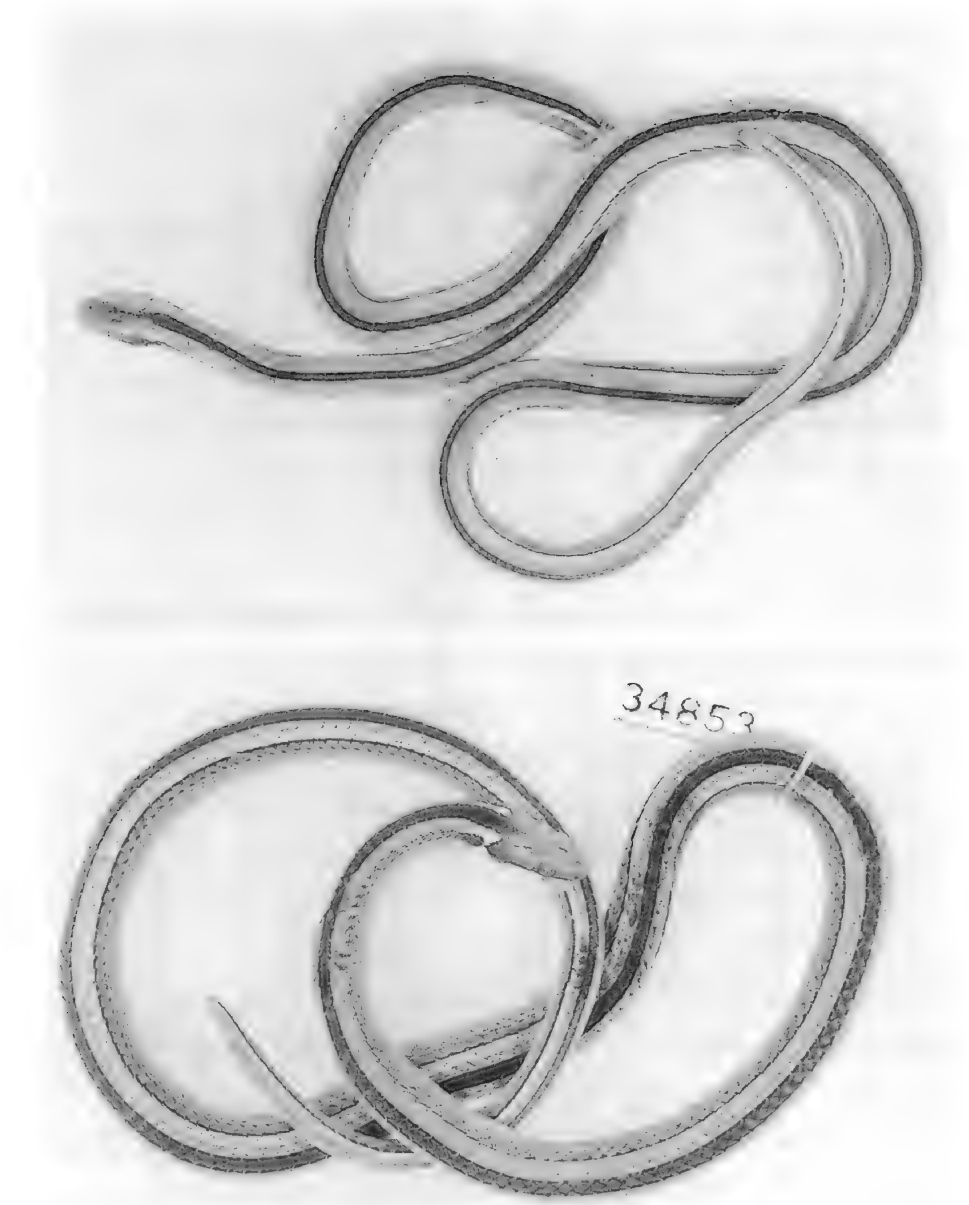

Fig. 6. *Psomophis genimaculatus* (Boettger). **Top:** Lectotype (BMNH 1946.1.5.83) from an unknown locality in Paraguay. **Bottom:** Specimen (CM 34853) from southeastern Bolivia. Approximately ×1.2.

preserved specimen and Boulenger's (1894a: 171) mention of a pink ventral stripe suggest that the ventral surfaces are brightly colored in life.

NATURAL HISTORY: A specimen (USNM 331437) found sunning on a road contained in the esophagus partially digested remains of two small hylid frogs, these presumably having been partially regurgitated after the snake was captured. Another specimen (IE 1097) contained well-digested remains of a hylid frog similar to those in USNM 331437. A female (CM 94228, 373 mm SVL) collected in October contained six oviductal eggs; one of uncertain date (CM 34852, 332 mm SVL) had seven developing follicles.

E. J. Censky (in litt.) reported finding a specimen (CM 94228) in thorn-scrub in Par-

aguay. Strussmann and Sazima (1993: 158) recently described the Brazilian Pantanal habitat of *Psomophis "joberti"* (presumably = *P. genimaculatus*, see Remarks below) as follows:

> most areas are large, open plains covered by native grasses . . . and low bushes during the dry season, and by aquatic vegetation during floods. When flooded, water depth varies from a few centimeters in the open fields to more than a meter in adjacent permanent swamps, water channels and ponds . . . The forested formations are usually found in patches ("capões") or strips ("cordilheiras") of non-flooded higher ground interspersed throughout the Pantanal lowlands.

Nineteen species of colubrids occurred in the above Pantanal assemblage. Nine specimens (about 4% of total snake specimens) of *Psomophis* [*genimaculatus*] were collected over a period of approximately 15 months, and it ranked seventh in relative frequency of occurrence. It was found predominantly in the forested areas (less frequently in deforested areas), rather than in the more extensive open plains (Strussmann and Sazima, 1993: table 1). Frogs and lizards were recorded in the diet. The species was characterized as diurnal and "semiarboreal," the last term being unexplained.

REMARKS: Boettger was in correspondence with Boulenger (e.g., as shown in Boettger, 1885b) and one of the three syntypes of his *genimaculatus* was sent to the British Museum of Natural History (Boulenger, 1894a: 170 [specimen "*a*"], to later be designated as the lectotype by Hoge (1958). *Psomophis genimaculatus* (Boettger) is somewhat similar to *Psomophis joberti* in color pattern and nearly all aspects of scutellation, leading Hoge (op. cit.) to place the junior name (*genimaculatus*) in synonymy. Indeed, we can find no substantive scutellational differences suggestive of two forms in the specimens available to us, all the more remarkable given the distribution of specimens across much of South America south of the Amazon basin (fig. 1).

We resurrect *Psomophis genimaculatus* (Boulenger) for the Bolivian, Paraguayan, and Brazilian Pantanal populations of this complex based on a distinctive and geographically coherent color pattern. All specimens examined from Bolivia and Paraguay, and one from extreme southwestern Brazil, have a distinct curvature of dark pigmentation around the angle of the jaw (fig. 5A), whereas this marking is lacking in specimens from more easterly parts of Brazil, where the dark postocular color extends in a straight (or slightly curved) line onto the neck (fig. 5B). Other pattern differences are more subtle and variable: In *P. genimaculatus*, the lateral body stripe often fails to reach the head, being usually interrupted by a pale collar (broken at the midline); on the anterior body, the upper edge of the lateral stripe either fails to reach scale row 5 or touches only the lower edge of row 5. If the lateral stripe of *genimaculatus* does reach the head, remnants of the pale collar are seen as relatively distinct nuchal spots, on each side of the vertebral stripe and sometimes also on the lower side of the neck below the lateral stripe. *P. joberti* seems never to have a pale collar, although pale nuchal spots may be faintly indicated; the upper edge of the lateral stripe anteriorly always involves row 5 in *P. joberti*, although the lateral body pattern is generally more variable and often less well defined in *joberti*. *Psomophis genimaculatus* may have a slightly lower modal number of prediastemal maxillary teeth than *P. joberti*, but any difference is slight (see Osteology above).

Psomophis genimaculatus may occur sympatrically with *P. obtusus* in the vicinity of Asunción, Paraguay, where the Guaraní name *ñuasó* was said to be shared by these and other small snakes (Gatti, 1955: 96).

Most Brazilian references to *Rhadinaea* or *Liophis genimaculatus* are based on the species *Psomophis joberti*, but one reference (Koslowsky, 1898a), for a locality in the Brazilian Pantanal, probably was based on true *genimaculatus*, as was most likely a record (Strussmann and Sazima, 1993) of *Liophis joberti* from the same region. We have examined one Brazilian specimen (UMMZ 108764) of *P. genimaculatus*, which was obtained in 1941 at Porto Esperança on the Rio Paraguay, deep in the Pantanal as confirmed by J. R. Bailey (personal commun.).

The distribution of *Psomophis* in Argentina is confused (see also Remarks for *P. obtusus*). We have not seen specimens of *P. genimaculatus* from Argentina and the species has disappeared from recent checklists of Argentine snakes. Koslowsky (1898b: 193) reported *genimaculatus* from Corrientes,

Gran Chaco, and Misiones, and Serié (1921, 1936) listed it from Chaco, Corrientes, Misiones, and Santa Fé. But it is not mentioned in Abalos and Mischis (1975), Williams and Francini (1991), or Cei (1993).

The distribution of specimens of *genimaculatus* which we have examined (fig. 1) corresponds closely to the delimitation of two major physiographic regions of South America—the Llanos de Mojos of eastern Bolivia, and the Chaco Boreal (including the Pantanal) of southern Bolivia, southwestern Brazil, and northern Paraguay (Sarmiento, 1983; Solbrig, 1976; see also Short, 1975, and P. Myers, 1982).

Psomophis joberti (Sauvage), new combination

Figures 2, 4, 5B, 7, 8, 10A,B

Enicognathus Joberti Sauvage, 1884: 146 (type locality, "Marajo, Amazone" [Ilha de Marajó, Pará, Brazil]).

Rhadinaea undulata (not of Wied): Boulenger, 1894a: 174, part (*Enicognathus joberti* Sauvage listed questionably as a synonym).

Liophis genimaculatus (Boettger), part (reference to Brazil): Amaral, 1929a: 88; 1929b: 172; 1936: 114.

Liophis joberti (Sauvage): Hoge, 1958: 222–223. Peters and Orejas-Miranda, 1970: 178.

HOLOTYPE: MNHN 5353 (figs. 7, 10A), a female in fair condition; 343 mm total length, 66 mm tail length, with 207 ventrals and 60 pairs of subcaudals.

DIAGNOSIS: *Psomophis joberti* is a pale brown snake with contrasting dark head coloration, which is posteriorly confluent with a vertebral dark stripe; there also are lateral lines or stripes, but the striped pattern is often vague. It resembles *P. genimaculatus* in having 17 scale rows at midbody (vs. 19 in *P. obtusus*) but differs in details of color pattern: *P. joberti* has the dark postocular/temporal coloration continuing in a straight line onto the neck (a dark wedge of color extending anteriorly under corner of mouth in *genimaculatus*), it lacks pale nuchal markings or has at most only very indistinct nuchal spots, and it has the uppermost lateral line or stripe involving up to one-half of scale row 5 (at most, only the ventral edge of row 5 in *genimaculatus*).

DISTRIBUTION: Eastern Brazil. The species appears to occupy an extraordinary array of habitats, although it possibly has a disjunct distribution that excludes Amazonian forest (see Remarks).

DESCRIPTION: Largest specimen a female 443 mm total length, 81 mm tail length; largest male 383 mm total, 76 mm tail. Tail 17–24 percent of total length (17–20% ♀, 20–24% ♂). Ventrolateral edges of body weakly angulate. Dorsal scales in 17-17-15 rows (rarely 15-17-15), with reduction occurring through loss of row 4 or fusion of 3 + 4. Ventrals 192–216, averaging higher in females but with broad overlap (12♂ 192–206, $\bar{x}$ = 199.0 ± 3.91; 17♀ 195–216, $\bar{x}$ = 203.1 ± 6.74). Subcaudals 51–71, much higher in males (12♂ 59–71, $\bar{x}$ = 65.2 ± 3.27; 16♀ 51–60, $\bar{x}$ = 54.3 ± 2.49). One preocular, two postoculars, 1 + 2 temporals, eight supralabials (2–3 in loreal, 4–5 in orbit), usually 10 (9–11) infralabials.

Light brownish body with a usually black-edged median dark stripe (vertebral row and adjacent edge to ½ of each paravertebral row) extending from dark head for length of body, tending to fade near end of tail. The median stripe often is emphasized by a line of white dashes lying against the outside black edging. On either side of the vertebral stripe, the adjacent 1½–2 dorsal scale rows normally vary from slightly to noticeably darker brown than the sides of the body—but, in occasional specimens, the median five scale rows are exceptionally heavily suffused with dark pigment, which forms a broad, ill-defined, median stripe that may largely obscure the narrower vertebral stripe (fig. 8).

Top and upper sides of head overall black—or dark brown on top and blackish brown on sides, the darker lateral color forming a stripe extending from tip of snout through eye and continuing to side of neck either in a straight line (fig. 5B) or with a slight ventrad curvature (fig. 10A, B). Usually no definite pale nuchal spots, although ground color often somewhat paler behind dark head cap on either side of vertebral stripe.

Lateral dark lines and stripes varying from distinct to vague, but a blackish line starting anteriorly on scale row 5 and continuing to end of tail is characteristic: This black line is the top edge of an often discrete lateral stripe (continuous with lateral head stripe), ante-

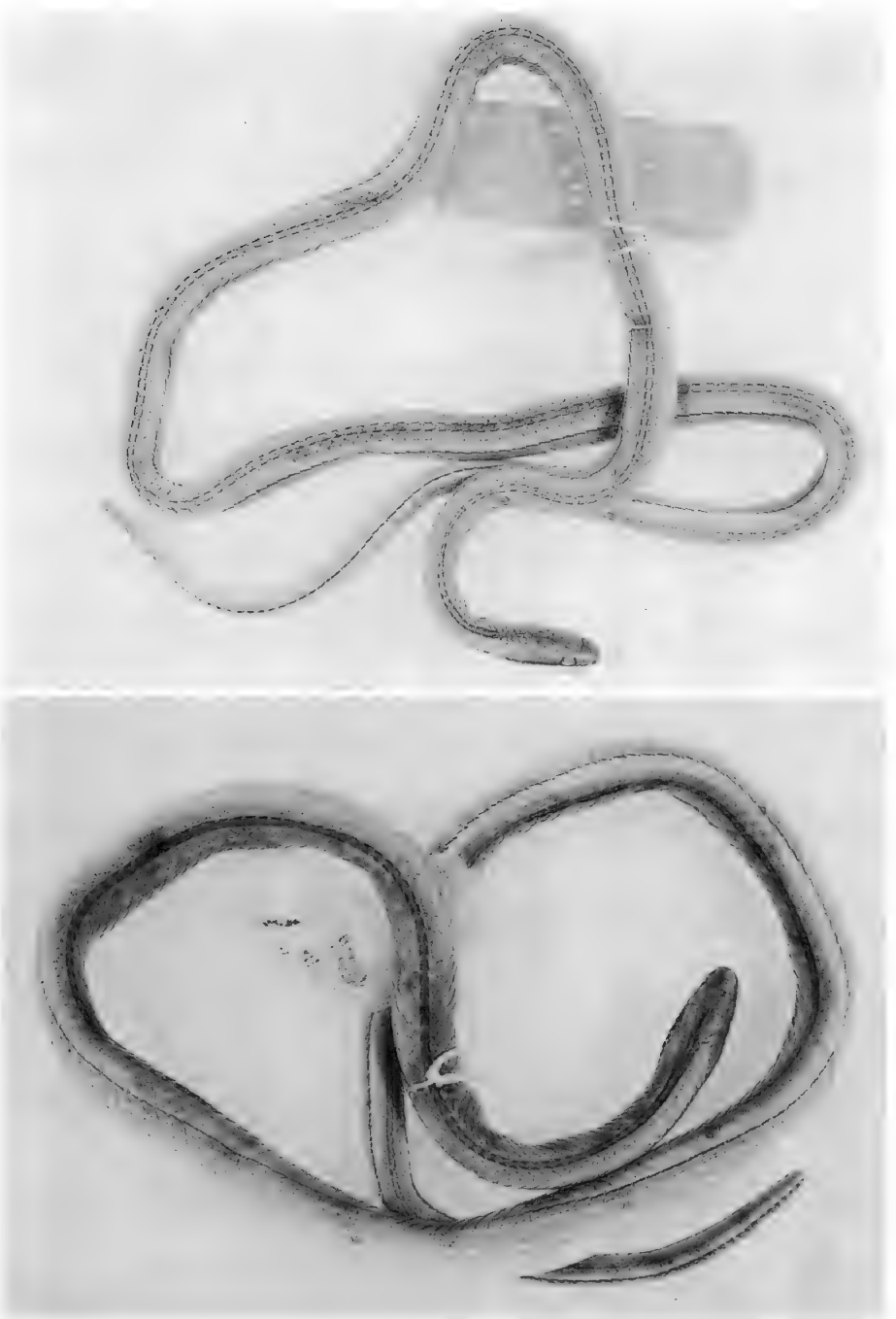

Fig. 7. *Psomophis joberti* (Sauvage). **Top:** Holotype (MNHN 5353) from Ilha de Marajó, mouth of the Amazon. **Bottom:** Specimen from Atlantic forest of extreme eastern Brazil (MZUSP 5178, Ponta de Pedras, Paraiba). Both about × 1.2. Compare figure 8.

riorly on rows 4–5, posteriorly dropping to mainly row 4 or rows 3–4 (row 5 sometimes remaining involved, on lower edge) before continuing to end of tail. Also discernible in some specimens, a lower and broader, but fainter, grayish brown stripe anteriorly occupying adjacent halves of rows 2–3, 3–4, or 2–4, posteriorly dropping mainly to adjacent

Fig. 8. *Psomophis joberti* (Sauvage). A cerrado specimen (MZUSP 2160♀) showing a dark head cap and a broad median suffusion of pigment that largely obscures the narrow vertebral dark stripe, about ×1.2. Such intensification of melanophores in the median 5 scale rows has no obvious geographic, sexual, or ontogenetic correlation. Two other female specimens, one smaller and one larger, from the same locality (Aruaña, Goias) had normal dorsal patterns. Compare figure 7.

halves of rows 2–3. Fusion of the two lateral stripes may give impression of a single poorly defined grayish stripe on rows 2–5, edged above by the black line on middle of row 5—with a pale thin center developing posteriorly to separate two stripes on rear of body, the lowermost on rows 2–3 and the uppermost mainly on row 4. Or only remnant edges of stripes remaining, resulting in a pattern of faint brown lines on first several scale rows. A dark brown line always on row 1.

Supralabials and ventral surfaces white, essentially immaculate except that tips of posterior ventrals sometimes weakly dotted with dark.

NATURAL HISTORY: Hoge (1952a: 199) listed *joberti* as diurnal and terrestrial in the cerrado and campo (savanna). One female (MCZ 3000, 326 mm SVL), month of collection unknown, contained four shelled eggs.

REMARKS: Although *joberti* was named in 1884, it was not recognized as a wide-ranging, eastern Brazilian species until 74 years later, when Hoge (1958) resurrected the name based on his examination of the holotype. In the interim it was variously reported from Brazil under the names *Rhadinaea genimaculata* or *Liophis genimaculatus* (Amaral, 1929a, 1929b, 1936; Schmidt and Inger, 1951; Hoge, 1952a, 1952b). Hoge (op. cit.) also designated the lectotype for *genimaculatus*, which he unfortunately considered synonymous with the older name *joberti*; thus, the two species have remained confused until now (see discussion under *P. genimaculatus*).

The scattered localities (fig. 1) for specimens of *Psomophis joberti* cover an extraordinary range of major habitats, including the northern portion of the Atlantic forest (fig. 1, locality 4), forest enclaves (3,6), caatinga (5,7,8), and cerrado (9,11,12). We are unaware, however, of any definite localities from Amazonian forest, leading us to suspect that the Marajó Island population (locality 1, the type locality) may be disjunct from the rest of the range. Cunha and Nascimento (1978) did not list the species as part of the snake fauna of the adjacent mainland east and south

of Marajó Island. The Marajó locality itself is not suspect because, in addition to the holotype (fig. 7), a second specimen was obtained from there by Emílio Augusto Goeldi prior to 1895 (BMNH 95.3.29.14, Boulenger, 1896: 635, as *R. genimaculata*), about the time that he became director of the Museu Paraense.

Although several specimens are from localities within caatinga (5, Lima Campos; 7, Barreiras; and 8, Pirapora), *Psomophis joberti* may not be a characteristic inhabitant of this semiarid environment. Vanzolini collected *joberti* in a mesic forest isolate (our locality 4, see Vanzolini, 1981) in northeastern Brazil, but it was not found in the surrounding caatingas (Vanzolini et al., 1980; Williams and Vanzolini, 1980: 100). The Lima Campos locality (5), although in the caatingas, is the site of a very large irrigation dam and so has relatively mesic features marginally (P. E. Vanzolini, in litt.).

Several additional localities can only roughly be associated with a major habitat according to P. E. Vanzolini (in litt.), who supplied the following information: Papary, now Nisia Floresta (2), near the coast, still has good soils and may have been Atlantic Forest in recent geological time, but it is now bare. Santa Isabel do Morro (10), on the river island of Bananal, is fundamentally cerrado, but with the possibility of gallery forest. The Ilha Solteira dam site (13) lies between the states of São Paulo and Mato Grosso do Sul; the São Paulo side used to be forest, but, by the time that the dam was built (and the specimen collected), it already was entirely given over to agriculture and pasture; the Mato Grosso do Sul side was and still is an ample (ca. 20 km wide) river flood plain devoted to cattle.

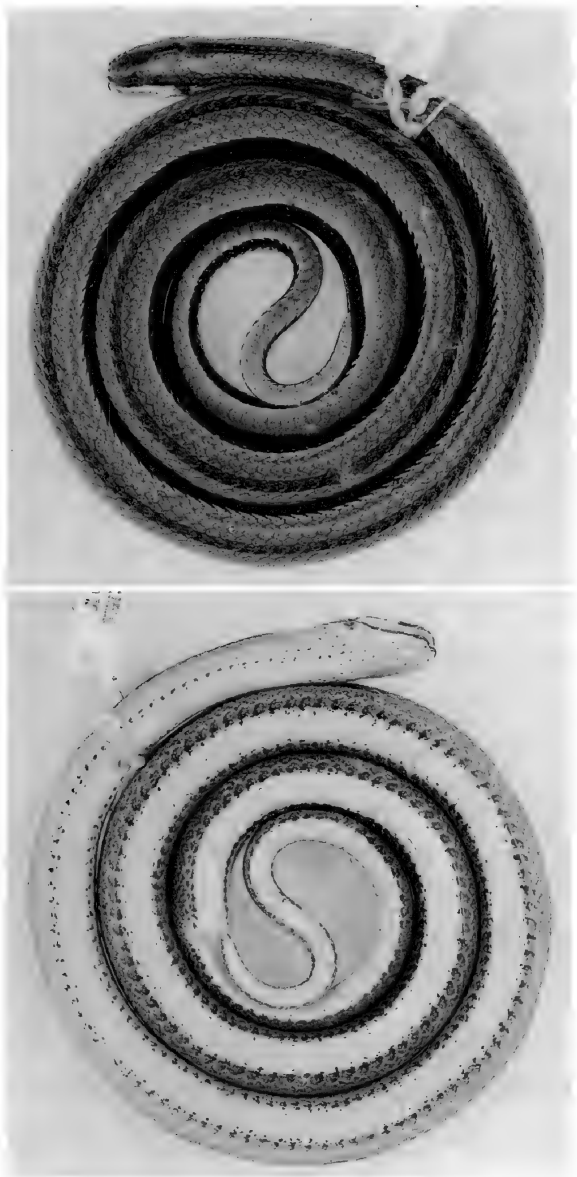

Fig. 9. *Psomophis obtusus* (Cope). Dorsal and ventral views of a specimen (CM 55413) from southern Uruguay, about ×1.0. This is the only species of *Psomophis* in which the lateral tips of the ventral and subcaudal plates are heavily marked with dark pigment from the sides of body and tail.

Psomophis obtusus (Cope), new combination

Figures 5C, 9, 10C

Rhadinaea obtusa Cope, 1863: 101 (type locality: Paysondu [Paysandú], Uruguay). Boulenger, 1894a: 171. Cei, 1993: 670–674, pl. 116.

Enicognathus Jan (*Rhadinaea* Cope) sp., Müller, "1882" [1880]: 144.

Coronella obtusa (Cope): Boulenger, 1885: 194; 1886: 430–431.

Liophis obtusus (Cope): Amaral, 1929a: 89; 1929b: 173; 1936: 115. Vaz-Ferreira and Sierra de Soriano, 1960: 35. Peters and Orejas-Miranda, 1970: 179.

HOLOTYPE: Originally a United States National Museum specimen but now lost. This was one of three new species obtained by H.

W. Kennedy at Paysandú and described in Cope's 1863 paper, the other two being *Pantodactylus bivittatus* and *Rhadinaea poecilopogon*. The last two but not the specimen of *obtusa* are listed in Cochran's (1961) catalog of type specimens. R. P. Reynolds (in litt.) searched USNM data sources and could find no indication that the *Rhadinaea obtusa* specimen had ever been cataloged. The lost holotype probably was a large female in excess of 410 mm total length, with the tail comprising probably about 21 percent of the total (see Remarks).

DIAGNOSIS: *Psomophis obtusus* differs from its two congeners in having 19-19-17 dorsal scale rows (vs. 17-17-15), and also is readily distinguished by details of color pattern: *P. obtusus* has the dark vertebral stripe (at least traces of it) beginning at the snout rather than at the rear of the head, and the sides of the body posteriorly become dark colored to the tip of the tail. It tends also to have fewer ventrals, more subcaudals, and a somewhat longer tail, which, although thickened, is not so abruptly pointed as in *genimaculatus* and *joberti*. *P. obtusus* also differs in being ventrolaterally rounded (nonangular, see footnote 8).

DISTRIBUTION: Southern Brazil, southern Paraguay, Uruguay, and adjacent northern Argentina (see Remarks).

DESCRIPTION: Largest specimen a female 416 mm total length, 82 mm tail length; largest male 404 mm total, 114 mm tail. Tail 20–28 percent of total length (20–24% ♀, 23–28% ♂). Ventrolateral edges of body rounded. Dorsal scales in 19-19-17 rows, with reduction occurring through loss of row 4 or fusion of 4 + 5. Ventrals 171–191,[14] higher in females but with broad overlap (3♂ 171–188, $\bar{x} = 179.0 \pm 8.50$; 8♀ 175–191, $\bar{x} = 184.1 \pm 5.82$). Subcaudals 57–83, averaging higher in males (3♂ 64–83, $\bar{x} = 74.7 \pm 9.71$; 7♀ 57–75, $\bar{x} = 66.6 \pm 6.40$). One preocular, two postoculars, 1 + 2 temporals, eight or rarely seven supralabials (2–3 in loreal, 4–5 in orbit), usually 10 (8–11) infralabials.

Pale brown dorsally, with a median brown stripe usually starting on snout and fading away on base of tail. Median stripe tending to be weak and irregular on head, becoming well defined with black edges on body, where it occupies the vertebral and up to half of each paravertebral scale row. A black line on rostral widens on each side of head to form a blackish brown stripe that passes through eye and above corner of mouth, where a ventrad extension of dark pigmentation extends straight down, isolating pale supralabial area from pale throat color.[15] No pale nuchal spots or collar.

Lateral head stripe abruptly narrows on neck to a black line on edges of rows 5–6 or middle of row 5. Sides of body and tail below black line posteriorly varying from dark chocolate brown to blackish brown, sometimes dark enough to obscure line on row 5.

Supralabials and underside of head white or yellowish—immaculate or sparsely dotted with black. Median ventral surfaces immaculate white or yellowish. Tips of ventrals under neck immaculate or dark dotted, the ventrals and subcaudals otherwise moderately to broadly tipped with dark color from lower sides. A colored painting of *obtusus* (Amaral, 1978: 105) shows grayish brown sides and middorsal stripe on a grayish ground color, with a pale yellowish tan venter; but there is no indication of stripes on the head.

NATURAL HISTORY: One specimen (CM 55413) was found under a piece of trash at midmorning in a "sandy area with low hills (probably fossil dunes), much disturbed with many borrow pits where sand has been removed for construction use" (C. J. McCoy, in litt.). Vaz-Ferreira et al. (1973) reported "arthropods" in the stomach of one specimen and "several *Hyla*" in another. Amaral (1978: 105) stated that in southern Brazil *obtusus* "lives in open fields hunting for insects and frogs in general."

[14] Ventral counts are 182–193 in four unsexed hatchlings. Juvenile snakes often are found to have counts outside the normal ranges for adults, for which reason caution needs to be exercised when using such data taxonomically (Myers, 1974: 26, and contained references).

[15] This marking appears to develop ontogenetically in *Psomophis obtusus*: In four hatchings 96–107 mm SVL (CM 56870–56871, 57085–57086) the pigment barely extends ventral to the mouth line, but does cover nearly all the ultimate infralabial. In a slightly larger individual (CM 57084, 167 mm SVL) the pigment covers not only the last infralabial, but also about half of two adjacent gular scales, with slightly more of the adjacent gular scales tending to be covered in adults.

Vaz-Ferreira et al. (1970, 1973), investigating the use of ant nests as oviposition sites by squamates in Uruguay, found that clutches of *Psomophis obtusus* eggs were second only to those of *Philodryas patagoniensis* in frequency of encounter in nests of three species of *Acromyrmex*. Fifty-three *P. obtusus* clutches contained 3–18 eggs (average of 7.5), but at least the higher numbers certainly represent communal clutches—the efforts of several females at a common nest site.

Psomophis obtusus eggs were found between December and February. Of two adult females found in ant nests in early December, Vaz-Ferreira et al. (1973) reported six shelled oviductal eggs in one (370 mm SVL) and an unstated number of "small unshelled oviductal eggs" in the other (392 mm SVL). One female which we examined contained five shelled eggs (USNM 73431, 303 mm SVL, month of collection unknown).

REMARKS: There currently is no "complex zoological problem" requiring recourse to an extant type specimen of *Psomophis obtusus*, and neotype designation is therefore prohibited (Internatl. Comm., 1985: art. 75).[16] The lost holotype of *Rhadinaea obtusa* Cope (1863) probably was a very large female, but it is important to note that Cope's measurements of 41.25″ total length, 8.75″ tail do *not* denote inches (which are the units of measure in most of his work). The curious use in this paper of the symbol ″, followed either by some form of numeric fraction or by a whole number preceding the symbol ‴, conceivably represents the metric system. For example, Cope's (op. cit.) measurements for the holotype of *Rhadinaea poecilopogon* were 39⅔″ total length, 10⅔″ tail length; Myers' measurements of the same specimen, a century later, were 39.0 cm total, 11.2 cm tail length.

The type locality of *P. obtusus* is in Uruguay, and most of the specimens that we have seen are from that country, where the species was said by Devincenzi (1925: 32) to be relatively abundant.

The only Brazilian records of *Psomophis obtusus* known to us are those of Boulenger (1885, 1886, 1894a: 171), for a specimen (not examined) from an unspecified locality in Rio Grande do Sul, and Amaral's natural history note (see above) and illustration of a specimen presumably from the "Zona meridional" of Brazil. *P. obtusus* and *P. genimaculatus* may occur sympatrically near Asunción, Paraguay, where they were said by Gatti (1955: 96) to share the Guaraní name *ñuasó* along with several other small snakes.

As already mentioned under *P. genimaculatus* above, the known distribution of *Psomophis* in Argentina is confused. Neither *P. genimaculatus* nor *P. obtusus* is mentioned in a recent checklist of Argentine snakes (Williams and Francini, 1991), although at least the last species does occur (fig. 1). Boulenger (1894a: 171) mentioned a specimen of *obtusus* from Colonia Resistencia, C. Chaco [probably Resistencia, Chaco, Argentina; see Boulenger, 1889, for a report on the amphibians obtained by the same collector at this locality]. Koslowsky (1898b: 193) reported *obtusus* from Corrientes, Entre Ríos, Chaco, Misiones, Salta, and Tucumán—a distribution covering much of northern Argentina east of the Andes. In later catalogs of Argentine snakes, Serié (1921, 1936) gave the same provinces and territories as had Koslowsky. And Freiberg (1939: 8) repeated the range given by Koslowsky and Serié and, in addition, cited a museum specimen from Entre Ríos ("Pto. Algarrobo, Dep. La Paz"). Abalos and Mischis (1975) listed it as "Norte argentino." Cei (1993) gives the distribution of *P. obtusus* in Argentina as (our translation): "in [the province of] Chaco . . . in the littoral zone of Santa Fe, and probably in Entre Rios and Corrientes"—a distribution comprising basically the basin of the Río Paraná.

Among the few Argentinian specimens which we have examined (see Appendix) is one reputedly from "Patquia, Estancia de Breyer, La Rioja," a locality at the foot of the Andes. But the locality for this specimen (USNM 73431) was questioned in an emendation of the National Museum catalogs by P. E. Vanzolini, and is farther west than any other fully documented locality for *Psomophis obtusus* (fig. 1). The doubt stems from the uncertain origin of the collection containing the specimen, as documented in the National Museum accession records (we are

[16] Article 75 is among the most clearly written sections in the last few editions of the *International Code*, but, nonetheless, invalid designation of neotypes is not uncommon.

grateful to R. P. Reynolds for providing the following information about the collection): The collection was sent to the National Museum in 1927 by Alberto and Adolpho Breyer with no data except "Argentina." Subsequently (1940) Doris Cochran wrote to the Breyers requesting additional information about the collection, and, presumably as a result of their response (not located), she annotated the records for the entire collection with the locality "Patquia, La Rioja." Although the collection does contain many snakes typical for northwestern Argentina (e.g., *Lystrophis semicinctus*, *Liophis sagittifer*, *Oxyrhopus rhombifer*, *Philodryas burmeisteri*, *Bothrops ammodytoides*), some seem obviously to be from elsewhere (e.g., *Hydrodynastes gigas*, *Chironius exoletus*, *Leptodeira annulata*, *Sibynomorphus turgidus*, and probably *Micrurus corallinus*); see also comments by Dixon and Hendricks (1979: 18) concerning a specimen of *Typhlops brongersmianus*. Although we question the Patquia locality, we recognize that the distribution of *Psomophis obtusus* in Argentina is poorly understood at best.

RELATIONSHIPS OF *PSOMOPHIS*

INTRAGENERIC RELATIONSHIPS: Polarization of variable characters within the new genus is less than satisfactory without an explicit outgroup (see Intergeneric Relationships below), but we speculate that *Psomophis obtusus* is the plesiomorphic sister species of *P. genimaculatus* + *P. joberti*. It differs from *genimaculatus* and *joberti* in the following character states that we suspect to be primitive for this group: hemipenis more deeply divided and spines clustered (not distinctively arranged in four rows), nasal laminae of premaxilla apparently less developed, tail longer (20–28% vs. 17–24% of total length, sexes combined) and perhaps somewhat less abruptly pointed, 19 dorsal scale rows (vs. 17), fewer ventrals (171–191 vs. 189–216), and body ventrolaterally rounded (vs. angulate). The presumed derived states thus unite *genimaculatus* and *joberti* as sister species.

At first glance, the above scheme seems contradicted by a conspicuous feature of color pattern shared by *obtusus* + *genimaculatus*, namely the wedge of dark head color extending ventrad behind the corner of the mouth. However, intraspecific variation suggests that this unusual marking (fig. 5A,C) may be derived for the genus but subsequently lost in *joberti* (fig. 5B). The apparent ontogenetic development of the marking in *Psomophis obtusus* correlates with its derived nature. Near absence of the marking in occasional adult *P. obtusus* (fig. 10C) and its apparently vestigial presence in some *P. joberti* (fig. 10A,B) are thus regarded as atavistic expressions of separate ancestral conditions.

Intergeneric Relationships: The relationships of this small group of snakes are difficult to assess because, as with many other genera of Neotropical snakes, most easily discernible features appear either to be unique (autapomorphic) to the genus or else primitive within a larger group. The divided sulcus spermaticus places *Psomophis* among the "xenodontine" colubrids, but this dominant assemblage of the Neotropics as yet lacks persuasive documentation of either monophyly or paraphyly, requiring caution when it is treated as a unit for phylogenetic analyses (Cadle, 1984c, 1985). Nevertheless, two large assemblages within xenodontines—the Central American and the South American xenodontines (Cadle, 1984a, 1984b, 1984c)—receive some support as clades from microcomplement fixation studies of serum albumins.[17]

[17] In this paper, use of "xenodontines" with a Central or South American qualifier explicitly refers to these clades. There is very broad geographic overlap between these groups, which, however, clearly have their greatest generic diversity in Central America and in South America, respectively (Cadle, 1985). Dowling et al. (1983: table 10) used the available subfamily names Dipsadinae and Xenodontinae, respectively, for two "xenodontine" clades, based on an unpublished dissertation by J. V. Jenner. Dowling et al. (1983) did not provide definitions or diagnoses for these clades, but did place the genera they discussed into these groups. However, these generic placements conform to our interpretation of neither the immunological nor morphological data on these groups. Thus, their placement of *Diadophis* and *Carphophis* in the Xenodontinae (tribe Philodryini) is contradicted by their own immunological data, as well as those of Cadle (1984c), who specifically compared these genera with *Philodryas*. Likewise, their placement of *Alsophis*, *Farancia*, and *Heterodon* in the Dipsadinae (Alsophiini) is

Most genera of the Central American xenodontine clade are further characterized by the derived hemipenial features of (1) reduction or loss of bilobation, (2) (uni)capitation, and (3) distal division of the sulcus spermaticus.[18] These features, in conjunction with the supportive immunological data, are adduced as synapomorphies for this large clade of Neotropical snakes, despite secondary loss of one or more of them in isolated cases.

On the other hand, the South American xenodontine assemblage recognized by the immunological data as yet lacks substantive support from morphology, although particular subgroups within this larger clade do receive morphological support, for example Pseudoboini (Bailey, 1967; Jenner and Dowling, 1985; and Cadle, unpubl. data) and Xenodontini (Myers, 1986). Although some South American groups are supported by hemipenial synapomorphies, the hemipenes of snakes in this clade (s.l.) are nonetheless characterized by their relative primitiveness compared with those of Central American xenodontines. The South American groups mostly lack "normal" capitation (i.e., unicapitation is normally absent, although there may be a few instances of independent derivation from semicapitation), bilobation is generally well developed, and the sulcus sper-

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supported by neither immunological data (Cadle, 1984a, 1984b, 1984c, 1988), nor by hemipenial synapomorphies discussed herein and in Cadle (1984c). We suspect that part of our differences in interpretation results from the reliance by Dowling et al. (1983) on an oversimplified, and in some instances erroneous, interpretation of too few features of the hemipenis (capitation and sulcus division).

[18] The sulcus spermaticus divides on the distal half of the organ (Myers, 1973: 31), usually within or close below the capitulum when that is a discrete structure. Some genera of Central American Xenodontines (e.g., *Leptodeira* and its relatives *Eridiphas*, *Hypsiglena*, and *Imantodes*) have a single or nearly single sulcus spermaticus, interpreted here as a synapomorphic loss relating these genera within the Central American Xenodontine clade. *Cryophis*, a putative sister taxon to these other genera, retains the primitive condition of the sulcus spermaticus (Cadle, 1984c), whereas some, if not all, *Leptodeira* have a vestigial terminal division with very short branches. Loss of hemipenial bilobation and increasingly distal division of the sulcus spermaticus appear to be repeated trends in several genera of xenodontines.

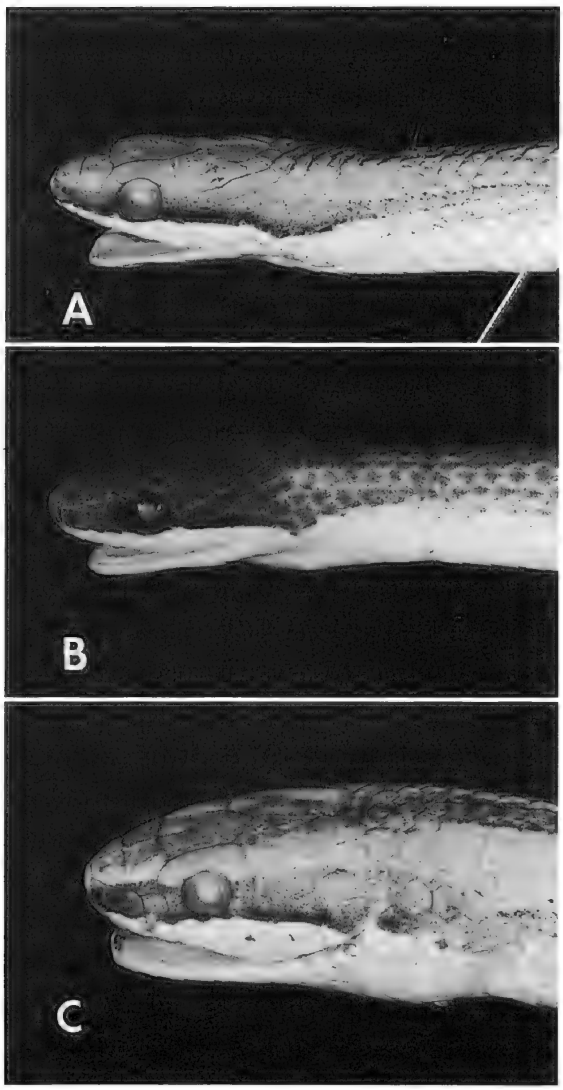

Fig. 10. Aspects of individual variation in lateral color pattern above and behind corner of mouth, all ×3.5. **A, B.** *Psomophis joberti* (A, MNHN 5353, holotype; B, MZUSP 2160). **C.** *Psomophis obtusus* (BMNH 1901.3.2.3).

The postmandibular ventrad extension of the postocular stripe in these specimens of *Psomophis joberti* (compare fig. 5B) may be a vestigial expression of a distinctive marking normally found in *P. genimaculatus* (fig. 5A) and *P. obtusus* (fig. 5C). Absence of the postmandibular marking in this specimen of *Psomophis obtusus* may be an atavistic expression of an earlier ancestral condition. See text.

maticus normally divides on the proximal half of the organ (Myers, 1973: 31). If, as postulated by Myers (1973: 31; 1974: 236), the unicapitate condition typical of Central American xenodontines (and approached in a few South American xenodontines) was derived by gradual shortening of a primitively bilobed organ and concomitant union (or consolidation) of their calyculate regions, then bicapitation, as seen in some South American xenodontines, is seemingly not a homologous condition. Rather, bicapitation would result from the opposite trend—retention of deep bilobation with distal retreat and restriction of calyculate regions to each head. Thus, although we recognize the South American xenodontines (sensu Cadle, 1984a, 1984c, 1985) as a clade based on the immunological data, we also recognize that a major task is testing of this hypothesis and identifying synapomorphies for the tremendous array of genera within this group.

In having a markedly bilobed hemipenis on which the sulcus spermaticus divides proximally, *Psomophis* associates with the genera of the South American xenodontine clade. But these are plesiomorphic features for this clade, and the relationships of *Psomophis* within that assemblage are not so clear. The hemipenial, osteological, and external characters which allow recognition of *Psomophis* are unique or virtually unique among South American xenodontines.

With respect to *Liophis* and *Taeniophallus* (ex "*Rhadinaea*" *brevirostris* group), the two genera with which species of *Psomophis* have generally been confused, we see no resemblances that could be interpreted as synapomorphies. The hemipenes of *Psomophis* are highly derived (bicapitate with centrolineal sulcus spermaticus, lobes with spinulate papillae, pseudocalyculate when retracted) but lack the derived features of *Liophis* (apical disks, which define the Xenodontini) and *Taeniophallus* (greatly reduced bilobation). As suggested earlier, the *Psomophis* hemipenis may have been derived from a deeply bilobed, acalyculate (?), distally spinose organ, but there seems no basis for deciding whether the primitive organ was bicapitate, semicapitate, or noncapitate.

The skull of *Psomophis* (figs. 2, 4) is the only other internal feature that we have investigated in any detail, but, with the exception of the premaxilla and its relationship to the nasals, the skull is fairly generalized. Moreover, a phylogenetic interpretation of skull osteology is rendered very difficult by the generally poor comprehension of skull morphology in South American (and other) colubrids. The form of most individual skull elements, excepting the premaxilla, is similar in most respects to skulls described for other (mostly much larger) "alsophiine" snakes, as represented by *Alsophis* and other West Indian colubrids (Maglio, 1970). These features include the shapes of the frontals, parietal, nasals, and prefrontals; the sphenoid bearing a long cultriform process and a high frontal crest; the separation of the postorbital from the frontal by a flange of the parietal; the emargination of the frontals and parietal around the orbital foramen; and the open trabecular groove. The broad groove present on the ventral surface of the cultriform process of the sphenoid of *Psomophis* is seen in some other xenodontines (*Imantodes cenchoa*, *Hydrops triangularis*) but is not usually developed to such an extent in small snakes such as *Psomophis*. One of the more unusual features of the *Psomophis* skull is the position of the anterior Vidian foramina near the border of the sphenoid and parietal, and the coincidentally long Vidian canals in this species, but we cannot now assign taxonomic significance to these features.[19]

We may hope that future studies of osteology and hemipenial morphology of South American xenodontines may shed more light on the relationships of *Psomophis*. Nonetheless, the premaxillary modification and especially the unusual features of the hemipenes seem unambiguously to point to the monophyly of this genus, a tightly knit group of three species that have more features in common than different.

[19] Underwood (1967) interpreted long Vidian canals as primitive within Caenophidians. But until further study of variation in this feature, including consideration of asymmetries noted within skulls of some species (Underwood, 1967: 17), it seems premature to generalize about the homology or derivativeness of particular states. Even among xenodontines (s.l.), there is considerable variation in the length of Vidian canals and in the position of associated foramina.

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APPENDIX: MUSEUM ABBREVIATIONS AND LOCALITY RECORDS

The following abbreviations of collections are used in the text and in the list of specimens examined.

AMNH	American Museum of Natural History, reptile collection, New York
BMNH	British Museum (Natural History), London
CM	Carnegie Museum, Pittsburgh
FMNH	Field Museum of Natural History, Chicago
IE	Instituto de Ecologia, Universidad Mayor de San Andres, La Paz
MCZ	Museum of Comparative Zoology, reptile collection, Harvard University, Cambridge
MNHN	Muséum National d'Histoire Naturelle, Paris
MZUSP	Museu de Zoologia, Universidade de São Paulo
UMMZ	University of Michigan, Museum of Zoology, Ann Arbor
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Psomophis genimaculatus

BOLIVIA: *Beni:* Prov. Ballivian, Espíritu [14°12′S, 66°37′W], IE 356, 851 [now USNM 331437], 1097; Guayaramerín [10°48′S, 65°23′W], USNM 280971; Trinidad [14°47′S, 64°47′W], MZUSP 8318. *Santa Cruz:* Prov. Chiquitos, San José de Chiquitos, 350 m [17°51′S, 60°47′W], CM 34852–34853 (see also Gans, 1960: 311); Santa Cruz [17°48′S, 63°10′W], UMMZ 69549. **BRAZIL:** *Mato Grosso:* two localities within 80 km radius S–SW Poconé [about 16°30′S, 56°45′W], Strussmann and Sazima (1993: 158, as *Liophis joberti*). *Mato Grosso [do Sul]:* Miranda [20°14′S, 56°22′W], Koslowsky (1898a); Porto Esperança [19°36′S, 57°27′W], UMMZ 108764. **PARAGUAY:** *No specific locality:* BMNH 1946.1.5.83 (lectotype). *Boquerón:* Filadelfia [22°21′S, 60°02′W], CM 94228; *Central:* Asunción [25°16′S, 57°40′W] (Boulenger, 1894a: 170; Gatti, 1955: 96).

Psomophis joberti

BRAZIL: *No specific locality:* MCZ 3000. *Bahia:* Barreiras [**7**,[20] 12°08′S, 45°00 W], UMMZ 108766. *Ceará:* Arajara [**6,** 7°21′S, 39°24′W], MZUSP 7225; Lima Campos [**5,** 6°25′S, 38°57′W], USNM 146613. *Goias:* Aruanã [**11,** 14°54′S, 51°05′W], MZUSP 2159–2160, 2171. *Mato Grosso:* confluence of Rio Araguaia and Rio Tapirapé [= Barra do Tapirapés, *q.v.*], Tapirapé village, AMNH 87960–87961; Barra do Tapirapés [**9,** 10°39′S, 50°36′W], MZUSP 4333–4335, 4406–4407, AMNH 93571–93573; Chavantina (Xavantina), Rio das Mortes [**12,** 14°40′S, 52°21′W], Hoge (1952b: 217); Porto Velho, Rio Tapirapés [**9,** 10°47′S, 51°00′W], MZUSP 3758–3760, 4659–4660; Santa Isabel [do Morro] [**10,** 11°34′S, 50°40′W], Hoge (1952a: 190). *Minas Gerais:* Pirapora [**8,** 17°21′S, 44°56′S], MZUSP 1163, UMMZ 108765. *Pará:* Marajo [= Ilha de Marajó, **1,** 01°00′S, 49°30′W], BMNH 95.3.29.14, MNHN 5353 (holotype). *Paraiba:* Gurinhém [**3,** 7°08′S, 35°27′W], MZUSP 8944; Mamanguape [**3,** 6°50′S, 35°07′W], MZUSP 3354; Ponta de Pedras [**4,** 7°38′S, 34°48′W], MZUSP 5178. *Rio Grande do Norte:* Papery [= Papary, now Nisia Floresta, **2,** 6°04′S, 35°08′W], Schmidt and Inger (1951: 459, as *Liophis genimaculatus*). *São Paulo (or Mato Grosso do Sul):* hydroelectric project on Rio Paraná, Ilha Solteira region [**13,** 20°25′S, 51°25′W], Hoge et al. (1974: 171).

[20] Boldface numbers 1–13 in the *P. joberti* localities correspond to numbered localities in the distribution map (fig. 1) and text discussion.

Psomophis obtusus

ARGENTINA: *Chaco:* Colonia Resistencia, C. Chaco [probably Resistencia, 27°27'S, 58°59'W], (Boulenger, 1894a: 171); *La Rioja:* Patquia [30°03'S, 66°53'W, but see text], USNM 73431. [*Santa Fé:*] Esperanza [31°27'S, 60°56'W ?], BMNH 1901.3.2.2–3. *Entre Rios:* Puerto Algarrobo, Dept. La Paz [30°38'S, 59°35'W], (Freiberg, 1939: 8). **BRAZIL:** *Rio Grande do Sul:* No specific locality (Boulenger, 1885, 1886, 1894a: 171). **PARAGUAY:** No specific localities (Bertoni, 1939). *Central:* vicinity of Asunción [25°16'S, 57°40'W], (Gatti, 1955: 96). **URUGUAY:** *Canelones:* Bañados del Carrasco [34°50'S, 56°03'W], CM 55413; National airport at Carrasco [34°53'S, 56°03'W], CM 57084. *Montevideo:* Montevideo [34°50'S, 56°03'W], USNM 65563; Peñarol [34°49'S, 56°11'W], CM 56870–56871; Santiago Vasquez [34°48'S, 56°21'W], CM 57085–57086. *Paysandú:* Paysondu [Paysandú, 32°19'S, 58°05'W], holotype (Cope, 1863: 101). *Rocha:* Between Rocha and Las Cano [= Lascano], near Paloma de la India Muerta [about 33°40'S, 54°00'W], FMNH 10354; Río Cebollati, Paso de Averias [33°36'S, 54°19'W], FMNH 10358. *Soriano:* No specific locality, BMNH 74.10.9.24. *Treinta y Tres:* 5 km NE Vergara [32°56'S, 53°56'W], AMNH 91518. [Many additional Uruguayan localities for *P. obtusus* are given in Vaz-Ferreira et al., 1970, 1973.]

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